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Biological Reference Points for Invertebrate Fisheries

[Points de référence biologiques pour la pêche aux invertébres]

INTRODUCTION / INTRODUCTION

Biological reference points for invertebrate fisheries: introduction[1]

Stephen J. Smith and Bernard Sainte-Marie

Abstract: In the context of applying the precautionary approach to fisheries management, much of the current attention on developing reference points has been focussed on finfish species. However, at present the largest marine fisheries in Canada in terms of landings and value are those for invertebrate species. A workshop on reference points for invertebrate fisheries was held in Halifax, Nova Scotia, Canada, from 2 to 5 December 2002 to address the particular needs of fisheries on this diverse group of species. Seven of the papers presented at that workshop were published as a group in this issue of the *Canadian Journal of Fisheries and Aquatic Science*. Reproduction and recruitment were identified by all of these papers as key elements of population resilience and productivity that needed to be monitored in some way. The monitoring of reproductive capacity should be extended to aspects important in the mating systems, such as local densities, spatial patterns of age–size structure, and spatial and temporal patterns of breeding areas for broadcast spawners with poorly mobile or sessile adults. Similarly, such monitoring would also include female and male size and the number of female reproductive opportunities for crustacean species with copulating adults.

Résumé : Dans l'application du principe de précaution à la gestion des pêches commerciales, la majorité des points de référence développés actuellement concernent des espèces de poissons. Cependant, au Canada, ce sont présentement les pêches marines d'espèces d'invertébrés qui sont les plus importantes en ce qui a trait aux débarquements et à la valeur monétaire. Un groupe de travail sur les points de référence pour les pêches commerciales d'invertébrés s'est réuni à Halifax, Nouvelle-Écosse, Canada, du 2 au 5 décembre 2002 pour étudier les besoins particuliers des pêches de ce groupe diversifié d'espèces. Sept des présentations à cette session de travail sont publiées ensemble dans ce numéro du *Journal canadien des sciences halieutiques et aquatiques*. Tous les auteurs ont reconnu le rôle primordial de la reproduction et du recrutement pour la résilience et la productivité des stocks; ils ont conclu que ces variables devaient être suivies d'une façon ou d'une autre. Le suivi de la capacité reproductive devrait être élargi aux aspects qui sont d'importance dans les systèmes d'accouplement, comme les densités locales, la variation spatiale de la structure de taille en fonction de l'âge, ainsi que les répartitions spatiales et temporels des aires de reproduction pour les espèces qui libèrent leurs gamètes au hasard et qui ont des adultes sessiles ou peu mobiles. Ce suivi devrait aussi inclure la taille des mâles et des femelles, ainsi que le nombre d'occasions de reproduction pour les femelles des espèces de crustacés chez lesquelles les adultes s'accouplent.

[Traduit par la Rédaction]

Publications on the precautionary approach to fisheries management stress the need for target and limit reference points (e.g., Garcia 1994; Haigh and Sinclair 1999; Rosenberg 2002). Reference points are usually defined with respect to some characteristic of the target population that is or can be monitored. The reference points themselves are values of this characteristic being measured that indicate in what state the population is likely to be. The states that we are most interested in with respect to current or proposed fishing strategies are whether or not the population is overfished, being overfished, or vulnerable to serious harm to its reproductive capabilities.

Currently, invertebrate fisheries are the largest fisheries on the eastern and western coasts of Canada in terms of land-

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[1]Derived from the Workshop on Reference Points for Invertebrate Fisheries, Halifax, Nova Scotia, 2–5 December 2002.
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ings and value. However, to date, much of the attention in Canada on reference points and the precautionary approach has been toward marine fish species and little has been focussed on invertebrates (Rice and Rivard 2002). Invertebrates as a group comprise species with widely different life history characteristics and types of fisheries. Moreover, benthic invertebrate populations often exhibit complex spatial structure and are prosecuted by fisheries that afford the opportunity for passive or active high-grading by sex, size, or aesthetic criteria, and market incentives exist to encourage these practices. This may make invertebrate resources more susceptible than most marine fish species to spatially or quality-based serial depletions against which generic, dynamic pool model based reference points offer little protection. Therefore, it is unlikely that many of the reference points being considered for fish species will be directly applicable to invertebrate species.

A workshop on biological reference points for invertebrate fisheries was held in Halifax, Nova Scotia, Canada, from 2 to 5 December 2002. There were a total of 59 participants from Argentina, Canada, Italy, New Zealand, the United Kingdom, and the United States. The primary goal of this workshop was to gather Canadian and worldwide experience on determining stock status and reference limits for one or more invertebrate species within predefined life history categories. In particular, we were interested in methods, approaches, or indicators for determining whether or not fishing activities are sustainable, resulting in overfishing, or causing serious harm to the reproductive potential of an invertebrate stock. The secondary goal was to provide a forum for the presentation of new methods and concepts for determining reference points for invertebrate species that are tied to specific aspects of their life history.

The proceedings from this workshop including abstracts and reports of the discussion groups were published in Smith (2003). The seven papers published in this issue of the *Canadian Journal of Fisheries and Aquatic Sciences* were commissioned before the workshop. The paper by Caddy (2004) provides an overall review of reference points with an emphasis on experiences to date with invertebrate species. The remaining six papers that were submitted were directed to present a comparison of the diversity of current and possible future approaches with respect to reference points for a specific species or group of species within a life history category that we had defined. Given the different life histories and types of fisheries, we expected that the definition of reference points would need to be tied very closely to life history characteristics of the species being fished. These life history categories were defined as follows and the papers in this issue associated with them appear in parentheses.

(1) Species with a larval dispersal phase and with poorly mobile adults that are broadcast spawners (e.g., sea cucumbers, sea urchins, abalone, swimming scallops, polychaetes including bloodworms, although some species do copulate). These species usually occur in beds and are highly fecund, and their habitat may be subject to disruption through fishing operations. (Botsford et al. 2004; Smith and Rago 2004)

(2) Species with a larval dispersal phase and with sessile adults that are broadcast spawners (e.g., bivalve molluscs, barnacles). These species also occur in beds and are highly fecund, and fishing operations may be very disruptive of their habitat. (Orensanz et al. 2004)

(3) Species with high fecundity, highly dispersive larvae, and mobile copulating adults that brood their eggs, usually with a large sexual size dimorphism (e.g., lobsters, crabs, shrimps). Fisheries either prosecute predominantly one sex or take special measures to protect egg-bearing females. Fishing operations may be disruptive of their habitat. (Cadrin et al. 2004; Fogarty and Gendron 2004; Siddeek et al. 2004)

(4) Species with direct development (no larval dispersal phase) and with copulating adults that are either mobile (e.g., squid) or poorly mobile (e.g., octopus, whelk, gammaridean amphipods). These species have low fecundity and are prosecuted by fisheries that are usually not disruptive of their habitat.

(5) Species not covered in the above categories or species about which little of their life history is known (e.g., medusae).

Invitations for submissions covering the last two life history categories were sent out, but unfortunately, no one was able to contribute.

Caddy (2004) notes that the reference points defined for marine fish species are usually restricted to catch, biomass, and fishing mortality. He suggests that the use of this limited set may partly explain the poor performance of associated harvest rules, especially in the face of environmental variability and ecological change and regime shifts. Given the diversity of life history characteristics listed above for commercial invertebrate species, a wider range of redundant variables representing empirical measures of stock condition and fishery productivity should be considered for monitoring and management. After all, productivity is a complex function of processes associated with reproduction and growth, and all are susceptible to environmental forcing. Caddy reviews some frameworks for integrating multiple indicators of stock condition into the assessment and decision process.

Three papers review reference points for species with broadcast spawning and sessile or poorly mobile adults. Botsford et al. (2004) evoke several unique aspects of sea urchin fisheries, e.g., tight ecological coupling and sheltering of juveniles beneath adult spine canopies. They indicate that the implementation of a limit reference point based on lifetime egg production would be desirable, although reference points based on logistic or surplus models and localization of macrophyte food resources currently exist. Geoducks are probably among the most long-lived of exploited animals, with the potential to reach in excess of 150 years. The retrospective analysis of age–frequency distributions by Orensanz et al. (2004) reveals that recruitment in the past declined to very low levels over several decades and a very large spatial scale. Because of the magnitude of recruitment variability and the sedentary nature of adults, these authors recommend a management approach relying on stock monitoring and data-based feedback rather than on model-based reference points. Smith and Rago (2004) show that "boom-and-bust" patterns of sea scallop abundance can be explained by the interaction of spatial patterns of habitat quality, distribution of fishing effort, and dispersal of larvae among patches. These

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three papers emphasize the importance of spatial aspects for species with poorly mobile or sessile adults and the likely effectiveness of natural refugia, reserves, or rotational fisheries for their management.

The remaining papers focus on crustaceans. In the case of pandalid shrimps, Cadrin et al. (2004) review a hierarchy of possible approaches to the development of reference points, from historical proxies culminating to the more elaborate stock–recruit and demographic production models, noting that reference points should evolve as the knowledge base grows. For crabs, Siddeek et al. (2004) derive harvest rate, effective spawning stock biomass, and total mature stock biomass reference points from a size-based model that incorporates specific life history and fishery characteristics in a stochastic or autocorrelated recruitment context. Both papers caution about the scarcity of information on stock–recruit relationships and other critical model parameters. Fogarty and Gendron (2004) note that the recent history of the long fishery for American lobster has been marked by a large, synchronous, and spatially extensive increase in productivity that remains unexplained. Nevertheless, they argue that lobster stocks are overfished and that complementary measures to reduce growth overfishing, increase the size or age range of spawners, and maintain or increase egg production relative to a threshold egg-per-recruit reference point are essential in the face of possible environmental change. As pointed out by Siddeek et al. (2004), none of the current model-based reference points incorporates the possibility of selection against phenotypes or genotypes with ecologically or economically desirable traits, i.e., fishing is assumed to be a neutral selective force.

Several common views emerged from all of the papers in this series. Reproduction and recruitment were identified as key elements of population resilience and productivity that needed to be monitored in some way. The impact of nonstationarity in production dynamics due, for example, to environmental change, density dependence, and modification of habitat suitability arising from changes in local densities suggests that the application of stock–recruit relationships needs to account for the prevailing population and environmental conditions. Therefore, the monitoring of reproduction capacity should be extended to aspects important in the mating systems such as local densities, spatial patterns of age or size structure, and spatial and temporal patterns of breeding areas for broadcast spawners with poorly mobile or sessile adults and to female size, male size, and number of female reproductive opportunities for crustacean species with copulating adults. In both categories of invertebrates, actual recruitment may depend on the spatial and temporal extent of nursery areas, density-dependent processes, and ecosystem interactions affecting growth and survival of cohorts through the larval and postsettlement phases, and monitoring of these variables in relation to environmental forcing is recommended. The importance of research for developing and improving reference points and indicators of stock condition was unanimously stressed.

Criticisms of the application of reference points for fisheries management have mainly concentrated on problems with model-based reference points because of the inability to accurately estimate population parameters and take into account the particular life history characteristics of the species being fished (Hilborn 2002; Mangel et al. 2002; Koeller 2003; Orensanz et al. 2004). The papers in this series have acknowledged the importance of being able to incorporate life history characteristics into model-based reference points, as well as exploring or expanding the use of a suite of empirical measures of stock or habitat conditions that relate directly to the biology of the concerned species and that can easily be conveyed to managers and stakeholders. In general, it was thought that model-based reference points would be useful as guidelines for proactive management, whereas routine, empirical measures of stock condition are essential for groundtruthing the outcome of management actions and promoting timely reaction to unexpected changes in stock condition.

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PERSPECTIVE / PERSPECTIVE

Current usage of fisheries indicators and reference points, and their potential application to management of fisheries for marine invertebrates[1]

J.F. Caddy

Abstract: The use of indicators in management of invertebrate resources is placed in the context provided by more extensive applications in finfish fisheries. Indicators proposed for the Convention on International Trade in Endangered Species based on extent-of-decline and trend analysis are appropriate should full assessments be unavailable. Measuring reproductive performance frequently builds on egg-per-recruit considerations, given that age structure and stock–recruit relationships are rarely available. Reference points derived from models are compared with direct use of data series, and a broad-brush approach providing a redundancy of indicators is recommended. Indicators may measure productivity as well as biomass and exploitation rate, but ecosystem, spatial, habitat, environmental characteristics, and socio-economic considerations also require monitoring. There is a need to integrate multiple indicators and limit reference points into harvest rules and other decisional infrastructures. The various driving force – pressure – state – impact – response classifications of indicators in use for environmental assessment are now being proposed for marine resources and offer one context for combining multiple indicators. Another is provided by the traffic light approach already used for invertebrate fisheries. The use of indicators and reference points in stock rebuilding is described.

Résumé : L'utilisation d'indicateurs pour la gestion des ressources d'invertébrés est placée dans les contexte des applications plus élaborées qu'on en fait dans les pêches des poissons à nageoires. Les indicateurs proposés par le Convention sur le commerce international des espèces de flore ou de faune sauvage menacées d'extinction basés sur l'importance du déclin et l'analyse des tendances sont adéquats lorsqu'il n'est pas possible de faire une évaluation complète. La mesure de la performance reproductive se base souvent sur le nombre d'oeufs par recrue, puisque la structure en âge et les relations stock–recrues sont rarement disponibles. L'utilisation de points de référence dérivés de modèles est comparée à l'utilisation directe des séries de données et il est recommandé d'utiliser une approche à large éventail qui fournit une redondance d'indicateurs. Les indicateurs peuvent mesurer la productivité ainsi que la biomasse et le taux d'exploitation, mais il faut aussi suivre les caractéristiques de l'écosystème, de l'espace, de l'habitat et de l'environnement et tenir compte des conditions socio-économiques. Il est nécessaire d'intégrer plusieurs indicateurs et points de référence limites dans les règlements de pêche et les autres infrastructures de décision. On propose actuellement diverses classifications de type force directrice – pression – état – impact – réponse des indicateurs utilisés dans l'aménagement de l'environnement pour la gestion des ressources marines et celles-ci offrent un contexte pour la combinaison d'indicateurs multiples. Une autre méthode est fournie par l'approche de type « feux de circulation » déjà employée dans les pêches d'invertébrés. L'utilisation des indicateurs et des points de référence pour la reconstruction des stocks est décrite.

[Traduit par la Rédaction]

Introduction

The collection of data series that support fish and invertebrate stock assessment is a practice that has begun to be formalized in recent years, with the concept of the fisheries indicator coming into prominence. The origin of this change in emphasis can perhaps be traced to the 1980s and 1990s when there was a paradigm shift from a focus on hitting target reference points (TRPs), the specific values of indicators for catch, biomass, and fishing mortality regarded as opti-

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mal, to a precautionary approach that aims to avoid undesirable conditions whose onset is measured by limit reference points (LRPs) (Caddy and Mahon 1995; International Council for the Exploration of the Sea (ICES) 1997; Serchuk et al. 1997), which progressively are measured in other variables, notably reproductive success. The use of indicators and LRPs in management procedures was highlighted by the United Nations Fish Stock Agreement and in parallel by the Food and Agriculture Organisation (FAO) Code of Conduct for Responsible Fisheries. Both regulatory instruments focussed attention on the use of LRPs as guides for management to be incorporated into harvest control rules or management procedures. This new approach reflects a growing appreciation of the low precision possible in determining resource status and hence the risks of overshooting targets. A more explicit role in management decision-making is now given to historical data series in the form of "sustainability indicators" (see FAO 1999; Anonymous 2000). These form elements of the precautionary approach, but as suggested in Department of Fisheries and Oceans (2000), other components incorporated into a fisheries "law" are essential, such that objectives are set, strategies to achieve them are planned and implemented, unacceptable outcomes are defined as LRPs, uncertainty is taken into account, system performance is monitored by indicators, and preagreement is sought from stakeholders on decision rules when limits are approached.

The actual and potential use of fishery indicators and associated reference points (RPs) in harvest control rules for invertebrates is the issue considered here. The "universe" of phenomena encompasses short-lived, motile species such as penaeid shrimps and cephalopods, longer-lived motile decapod crustaceans, and largely sedentary species (e.g., echinoderms, molluscs), some of which (e.g., precious corals) are very long-lived. Attempting to generalize is of course optimistic, considering the broad range of resources, fisheries, and regulatory frameworks that apply, but there are also common elements to the management problem that are also shared to a considerable extent with finfish resources. Among the dangers of extrapolating too freely from one type of resource to another, Seijo and Caddy (2000) and Gilbert et al. (2000) noted that fishery models generating RPs reflect value judgements in their basic axioms. Therefore, decisions on RPs and control laws derived from models whose axiomatic basis does not reflect the fishery context or life history in question can lead to inappropriate conclusions. This raises an alternative possibility of using appropriate indicator values as empirical RPs directly in control laws, and experience on this has been reported from the Southern Hemisphere (e.g., Gilbert. et al. 2000; Breen et al. 2002). In particular, routine application of dynamic pool models to marine invertebrates ignores factors of importance such as the spatial distributions of stock and fishing effort, a key issue for sedentary organisms. Implicit assumptions of stationarity in deriving and applying constant values for RPs may be especially misleading (see Jacobsen 1993) when only a few indicators are used for monitoring. This review therefore advocates use of a broad range of fisheries indicators and RPs to reflect life histories and fishery characteristics, ideally within a transparent fisheries harvest law understood and agreed to by managers and stakeholders.

The use of RPs in managing invertebrate fisheries has a short history so that reference to the more extensive finfish and environmental literature (e.g., Rice 2003) is inevitable. Progress so far with large-scale testing of management procedures on invertebrate stocks is limited (however, see Castilla and Defeo 2001); hence, experience with indicators, RPs, and harvest laws for other resources should be accepted only after careful consideration of the local and species context.

The process of defining indicators and RPs

A diversity of definitions

Indicators measuring events in an ecosystem have their origins in environmental assessment, and I discuss this usage first. Alfsen and Serbo (1993) defined an indicator as "a number that refers to the state, response or the development of important aspects of the environment ... is meant to give information in excess of what is directly measured or observed". Lenz et al. (2000) distinguished between an indicator and an index: "the latter is often constructed from several indicators, weighed together to describe ... the broader state of the environment". In a "Consultation on sustainable indicators for capture fisheries", Garcia and Staples (2000) defined a fishery indicator as "a variable, a pointer, an index related to a criterion. Its fluctuations reveal the variations in those key attributes of sustainability in the ecosystem, the fishery resource or the sector and social and economic well-being. The position and trend of the indicator in relation to the RPs or values indicate the present state and dynamics of the system".

So far in finfish harvest rules, indicators have tended to focus on monitoring fishing mortality, (spawning) biomass, and recruitment. For many invertebrates, the environmental linkage is often more predictive; for example, Barrett and Gillespie (1973) used rainfall, river discharge, and salinity as useful predictors of penaeid shrimp recruitment. Typically, very little of the wide variety of the fishery and environmental data collected routinely is used in deciding on fisheries management measures. Here, the problem is one of how to decide between first- and second-order effects on the managed population or fishery (Fig. 1) and how to organize multiple indicators so that their message is properly integrated and evident to nontechnical stakeholders and managers.

RPs should be regarded as critical values of indicators and may be derived from analysis, from observation, by expert judgement, or by comparison with data from earlier periods in the fishery when productivity was higher and sustained and also, but not exclusively, from population models. The following, based on Halliday et al. (2001), provides useful terminology relevant to the definition and use of indicators. (*i*) Elements of the fishery can be conceptualized as having "attributes" such as biomass, growth rate, natural mortality, accuracy of landing statistics, observance of mesh regulations, etc. (*ii*) A specific method of measuring time series of an attribute results in an "indicator". (*iii*) Groups of indicators that measure related processes are referred to as "characteristics". (*iv*) "Reference points" are values of indicators defined on some technical basis, which are believed to represent important changes in the fishery system. (*v*) Individual indicators may be assigned specific "weightings" and

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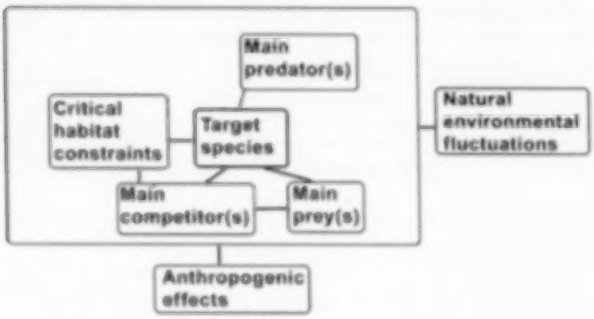
Fig. 1. Some first-order biological interactions directly affecting the managed population that could usefully be monitored in a multispecies fishery and (outside the box) several second-order factors affecting productivity.



"scaled" to normalize them. (*vi*) Individual indicators may be bundled into an "index", which represents the best measure of how a specific characteristic of the fishery is changing with time.

Whether generated from models or from experience, Gilbert et al. (2000) commented that "all the threshold RPs and conservative TRPs in the literature are likewise arbitrary". This is taken to mean that model-based RPs reflect expert judgement at two levels: (*i*) that the model is appropriate to the situation and species applied to and (*ii*) that the indicator value chosen as an RP has some relevance to events in the population, past, present, or future, as judged by experts. At some stage, then, a precautionary judgement must be made that when an indicator approaches an agreed LRP, this corresponds to an unacceptable risk of some negative event occurring. Such an acceptable level of risk must be decided on when reacting to critical indicator values (Prager et al. 2003).

The (D)PS(I)R approaches

Contemporary environmental concerns tend to classify indicators into functional categories, for example, measuring pressure, state, impact, and response (PSIR) (e.g., Malkina-Pykh 2000). Alternatively (FAO 1999; Garcia and Staples 2000; Gilbert et al. 2000), the categories may be reduced to a pressure–state–response (PSR) classification. A broader whole-system approach (see Zenetos et al. 2002) also incorporates economic or environmental "driving forces" into a holistic DPSIR approach aimed at also monitoring socioeconomic, marketing, and regulatory developments as opposed to just the biological components of the fishery system. There is little evidence that such a multiindicator approach to monitoring has yet been integrated into a fisheries management framework, but such a framework is proposed here (Fig. 2). As seen from the title of this section, the terminology is still fluid and practical applications in fisheries are limited. Although "state" indicators could be extended to include environmental, climatic, and pollution effects and multispecies or ecosystem issues, the single-species approach to formulating indicators, based strictly on the target species abundance and its degree of exploitation, still drives most fisheries management approaches.

A statistical framework for indicators and RPs

Managers and stakeholders need to be aware of, and express opinions on, the level of acceptable risk that a management measure will entail (e.g., see Francis 1993; Smith et al. 1993; Shotton and Francis 1997). Ensuring that there is only a low probability of LRPs being infringed requires a probabilistic framework, and Prager et al. (2003) focussed attention not only on errors in indicator values, but also on explicit decisions that need to be made by management on the acceptable level of risk that a LRP will be exceeded.

Normalized indicator values?

Prager (1994) noted the advantages of normalizing time series, or expressing indicator values in dimensionless form as a ratio of current to "optimal" values. Referring the current value of a population variable to some extreme value predicted by a population model (such as the ratio B_t/B_0 frequently used in production model based approaches) is one of a series of fisheries indicators proposed by Gilbert et al. (2000), but M.H. Prager (National Oceanic and Atmospheric Administration, National Marine Fisheries Service, 101 Pivers Island Road, Beaufort, NC 28516, USA, personal communication) suggests that normalizing to extremes of the range of values may incorporate errors into the indicator series, given that B_0 cannot be estimated directly for many exploited species. Using dimensionless or "normalized" indicators is nonetheless relevant, as fishery management is usually a relative procedure: managers rarely have access to the absolute values of fishing mortality rate or biomass in the current or even the previous management season. Thus, adjustments to the target F (or quota) for the next fishing period are often made relative to the indicator values (and quotas) that applied the previous season, and not from a completely new analysis.

If yield is an indicator, this can be "normalized" by comparison with the optimal value from a population model, e.g., maximum sustainable yield (MSY), or an RP representing earlier predepletion yield values. Examples from the literature include the "maximum average yield", which is the long-term average of past harvest levels, or the "maximum constant yield", variously defined as $0.2F_{0.1}B_0$, $0.5F_{0.1}B_U$; 2/3MSY, or cY_U by Annala (1993), in which B_U and Y_U are the "historic" values for biomass and yield prior to overexploitation and c is a "natural variability factor" that ranges between 0.6 and 1.0. Prior fitting of a Bayesian or stochastic model to catch data and repeated runs of the model may help determine how frequently these empirical RPs will be triggered in population management (e.g., Starr et al. 1997).

Prager et al. (2003) formulated indicators and RPs as ratios, which express the current fishing mortality F_{NOW} in relation to an indicator value that corresponds to optima or maxima (such as the MSY, F_{MSY}, or some other TRP). This removes the need to specify q, the catchability coefficient, which is difficult to estimate, and the problem of scaling is also reduced. This may also be appropriate for those indicators (e.g., fishing effort, nutrient runoff, etc.) that do not have a monotonically increasing effect on yield: this increases initially with the effort indicator but declines at high indicator values. Multivariate analysis of multiple time series to determine their functional relationship with fishing yield will in fact be required at some stage in the development of

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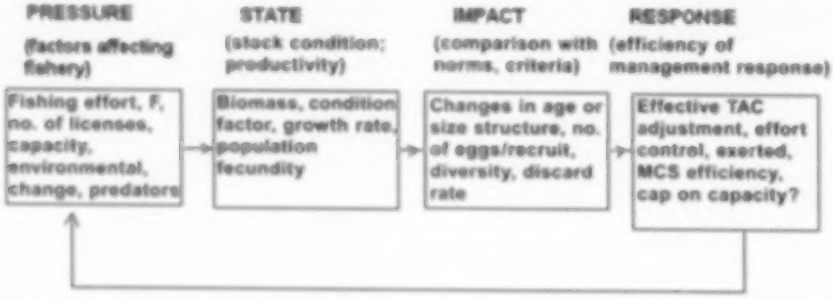
Fig. 2. One possible pressure, state, impact, and response (PSIR) framework for fisheries research and management envisaged in the context of an annual research and management cycle. TAC, total allowable catch; MCS, monitoring, control, and surveillance; *F*, fishing mortality.


PRESSURE
(factors affecting fishery)
STATE
(stock condition; productivity)
IMPACT
(comparison with norms, criteria)
RESPONSE
(efficiency of management response)
Fishing effort, F, no. of licenses, capacity, environmental change, predators
Biomass, condition factor, growth rate, population fecundity
Changes in age or size structure, no. of eggs/recruit, diversity, discard rate
Effective TAC adjustment, effort control, exerted, MCS efficiency, cap on capacity?

a set of indicators. An example of a management procedure using relative indicator values is the Magnusson–Stefansson procedure (Bell and Stefansson 1998) in which next year's quota is seen as a function of this year's yield and the biomass change δB since the previous year.

Errors in interpretation of indicators caused by the incorrect underlying model

Jones et al. (1996) noted that a clearly stated set of objectives is a prerequisite for formulating indicators, especially of ecological impacts: "The crux of habitat management is allowing or prescribing habitat changes that have desirable ecological effects and preventing or mitigating those changes that have undesirable effects" ... "Once these indicators have been determined ... design and implement a procedure for assessing the current status of the indicators, a benchmark against which future change can be contrasted". In addition to errors and biases in measuring variables contributing to the indicator, the choice and interpretation of indicators may be subject to serious errors of interpretation in that the indicator may not be indicate solely what was intended when the "characteristic" in question was defined. Some examples are provided here.

Example 1. Decreases in mean size

Monitoring mean individual size in the population as an indicator of past exploitation rate (which declines as older individuals are fished out by size-selective gear) may be confounded by exceptionally good recruitment. This adds to the argument for juvenile settlement and prerecruit indicators for species such as lobsters (Addison 1997).

Example 2

Mean trophic level was proposed as an index for measuring ecosystem effects of harvesting, namely "fishing down the food web" (Pauly et al. 2001). However, mean size, mean trophic level, and other outputs of food web models emerge as ambiguous measures of exploitation (Rochet and Trenkel 2003) compared with indicators of overall mortality rate or biomass and may decline if high productivity "inflates" the base of the food web as seems to have occurred in the Mediterranean (de Leiva Moreno et al. 2000). It would be more efficient (and less costly in sampling) to use survey data to establish indicators of changes in relative abundance of those predators feeding on the invertebrate species in question and establish a separate indicator monitoring recruitment or spatfall.

Example 3. Thinning

Thinning, a term used for populations of sedentary organisms (see Frechette and Lefaivre 1990), describes the process of actively culling small organisms in dense patches to increase the growth rates of survivors (the harvest of "cherry stone" clams after 1–2 years, leaving the survivors to grow more rapidly to "steamers", a policy giving two economic returns from the cohort). Disease (e.g., Klinck et al. 2001) and starvation can also lead to "self-thinning", which reduces density by intraspecific competition within dense "patches" without human intervention. Density and growth rate of sedentary molluscs are generally inversely related (see reviews in Caddy 1989), whereas natural mortality rate resulting from predator aggregation increases with density. From this perspective, fisheries models of the Beverton and Holt type, which assume that M is constant and independent of age and density, would give incorrect results. Monitoring density in these circumstances may provide a useful proxy indicator for growth and natural mortality rates.

Example 4

Bakun (1998) notes that some spawner–recruit relationships (SRRs) may be "artifacts" of alternating regimes of high and low productivity, with high and low recruitment occurring in different regimes for the same size of parental population. Hence, RPs based on the entire SRR data set may be misleading if stationarity in production is assumed, and recruitment levels should not be extrapolated from favourable to unfavourable regimes for a given stock size (Hilden 1988; Caddy and Agnew 2004). This disguised form of equilibrium thinking is fairly widespread in the literature and has been commented on unfavourably by Gilbert et al. (2000) and Seijo and Caddy (2000). Hilborn (2002) has also cautioned against an undue focus on technical RPs outside their management context.

Example 5

Most groundfish fisheries start after age 2 when predation mortality has largely occurred, but many invertebrate fisheries harvest immature animals for which natural mortality is higher than for adults. Thus, assuming constant natural mortality for juveniles in analytical models or virtual population analyses introduces a bias (see Stoner and Glazer (1998) for

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an example of a declining M vector for *Strombus gigas* and Caddy (1996) for a cephalopod example). When yield models incorporate a vector of M values declining to a constant level at around maturity, the advantages of minimum size regulations are reduced, but the reproductive value of older spawners is increased (see Caddy and Seijo (2003) for a hake fishery, but the principle also applies to long-lived invertebrates).

Categories of indicators and RPs

Different approaches to formulation of indicators and RPs

LRPs and TRPs are critical values of fishery indicators for population variables such as fishing mortality rate and biomass and a series of other biological, environmental, socioeconomic, and regulatory indicators. The following are definitions of common types of RPs following Caddy and Mahon (1995). TRP: "A Target Reference Point indicating a state of fishing and (or) resource which is considered to be desirable, and at which management action, whether during development or stock rebuilding, should be aimed". LRP: "A Limit Reference Point indicating a state of a fishery and (or) a resource which is considered to be undesirable and which management action should avoid".

The notation and use of RPs have since grown more complex, and two types of RP can be distinguished. A generic type of RP distinguishes the intention of the RP and specifies its role in a harvest law. The suffixes of generic RPs such as F_{buf} or B_{lim} (the fishing mortality rate seen as a buffer against overfishing and the lowest safe population biomass, respectively) are examples of this type. More specific or technical RPs such as Z_{1955}, F_{MSY}, $F_{0.1}$, etc., are derived from analysis of (earlier years) data or are outputs from models. Different definitions of generic RPs (e.g., F_{buf} and F_{pa}) have come into use in the North Atlantic Fisheries Organization (NAFO) (Serchuk et al. 1997) and in the ICES (e.g., Hilden 1993), with the ICES definitions showing perhaps a wider diffusion.

Indicators and RPs from trend analysis

A recent FAO technical consultation examined formal extinction criteria for inclusion of endangered aquatic species under the Convention on International Trade in Endangered Species (CITES) into appendix I (species threatened by extinction for which trade is forbidden) or into appendix II (species at risk of extinction unless trade is strictly regulated). Apart from existing CITES extinction risk criteria, the FAO background paper to the consultation (FAO 2001) suggested that indicators related to decline are the most relevant for marine fisheries resources. Three were proposed: (*i*) "recent-rate-of-decline" (the trend over the last 10 years is suggested; also see Musick 1999), (*ii*) "historical rate-of-decline" (the long-term trend over the time series), and, most importantly, (*iii*) "historical-extent-of-decline", which expresses current abundance as a fraction of some "historical baseline", which could be B_{MSY} (the biomass level shown to be capable of safely providing MSY as a sustainable yield), B_0 (the virgin biomass), or, as suggested in FAO (2001), the average of the four largest spawning biomasses in the historical time series.

Taxonomic position was considered by FAO (2001) as less important than life history characteristics in determining risk of extinction, and such characteristics seem well adapted to monitoring poorly studied species for which landing series are the main source of information. A historical rate of decline to 5–20% of the reference baseline, depending on species productivity, was recommended as a general guideline for listing in CITES appendix I, with 5–10% of the unexploited baseline values seen as a safety limit for species with high productivity, 10–15% for species with moderate productivity, and 15–20% for low-productivity species.

For potentially endangered species, FAO (2001) suggested projecting current rates of decline forward over a 10-year period to see if the result meets the above appendix I guideline for historical-extent-of-decline and concluded that historical-extents-of-decline not falling below 50% of the unexploited baseline should rarely be of concern. Given the wide variety of invertebrate life histories, a range of case-specific considerations could modify an overall evaluation based on rate- and extent-of-decline factors. These can be split into vulnerability factors (–) and mitigating factors (+), representing increasing or decreasing concern for the population (Table 1). Such a checklist could also be useful in deciding on indicator series and priorities for management action, as judgements on the need for immediate action will depend on specific life history vulnerabilities or the geographic and (or) socioeconomic situation. An alternative approach to classifying ecological effects of fishing on estuarine invertebrates (Blaber et al. 2000) suggests that indicators fall into the following categories: target and non-target organisms; nursery functions; trophic effects; habitat change and reduced water quality; human environment; and potential for local extinctions.

Other criteria prioritizing needs for conservation by species are given in Nielsen and Kenchington (2001). Although it would be desirable to base indicators on quantitative data, as noted in Seijo and Caddy (2000), an assessment of fishery status in a data-poor situation may use ranked or semi-quantitative criteria such as the scorings from questionnaires completed by experts (e.g., Caddy 1999*c*), comparable with ISO 2000 procedures for environmental assessment.

An example of trend analysis of invertebrate landings

Catch trend indicators for some 150 Mediterranean fish and invertebrates in a complex multispecies fishery were used by Fiorentini et al. (1997) to classify catch trends for which formal assessments were not usually available. These yielded useful indicators for management from catch trends over the short and long term, even without population analysis. As a first step, catch time series from the FAO database FISHSTAT-PC were sorted using a logical sequence of linear and polynomial testing and fitting procedures described in Fiorentini et al. (1997). Each 1950–1995 time series was allocated to one of 10 "shape categories" (Fig. 3) corresponding to segments of a sine curve. This classified for convenience a large number of time series into several long-term trend types, ignoring shorter-term periodicities and year-to-year fluctuations, while a linear trend was also calculated for the last 5 years of each time series (Fig. 4).

What emerged is that a small proportion of Mediterranean finfish and invertebrates fisheries show stable landings,

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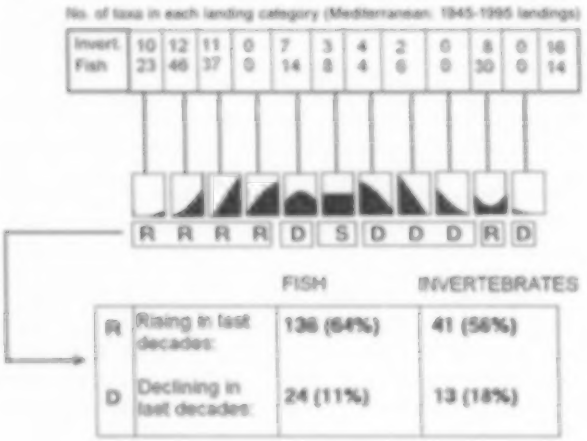
Table 1. Some supplementary factors to monitor that could change criteria based on trend analysis showing the direction of influence of the factor on population vulnerability (modified from FAO 2001).

Description of factor	Sign	Description of factor	Sign
Selectivity of removal (by species or size)	+	Low dispersal of gametes	–
Stock occurs in split jurisdictions	–	Specialized diet, habitat, or niche needs	–
Bycatch in fisheries for other populations	–	Aggregating behaviour or schooling	–
Vulnerable to capture by various gears	–	Endemism	–
Different vulnerability by sex (ratio)	–	Low genetic diversity	–
Source populations very vulnerable	–	Bottleneck in a life history stage	–
High vulnerability at a life history stage	–	Degradation or impacts on habitat	–
Nursery exposed to anthropogenic effects	–	Competing species increasing in size	–
Existence of spawning refugia	+	Predators heavily fished	+
High density critical to reproduction	–	High variance in recruitment	–
Hermaphroditism	–	Unfavourable environmental changes	–
Low fecundity	–	Stock near limits of latitudinal range	–

Fig. 3. Categorization of long-term landing trends by comparison with 11 overall trend configurations derived by dissecting a sine function into components (from Fiorentini et al. 1997). Numbers of species in each category are given for Mediterranean fish (Fish) and invertebrate (Invert.) species separately. The last box (16 and 14) corresponds to an intermittent category with gaps in the time series.


No. of taxa in each landing category (Mediterranean, 1945-1995 landings)
Invert. 10 12 11 0 7 3 4 2 0 8 0 16
Fish 23 46 37 0 14 8 4 6 0 30 0 14
R R R R D S D D D R D
FISH
INVERTEBRATES
R
Rising in last decades:
136 (64%)
41 (56%)
D
Declining in last decades:
24 (11%)
13 (18%)

Many species followed long-term upward trends until quite recently despite intensive fishing pressure. This rising trend since 1945 appears not just because of recent fishery developments: the Mediterranean has a long history of diverse fisheries including industrial-scale operations. Landing trends seem to reflect ecological changes underway in a semi-enclosed sea, not all as a result of overexploitation. An increase in productivity of the ecosystem seems the most likely explanation for continued upward trends over the last few decades of high exploitation rate (Caddy 2000). Increased nutrient inputs from densely populated catchment areas to this largely enclosed and formerly oligotrophic sea are documented (de Leiva Moreno et al. 2000). Steadily rising landings of *Venus gallina*, *Pecten jacobaeus*, *Nephrops norvegicus*, and *Squilla mantis*, species typical of fine sediments, of estuarine species (*Carcinus aestuarii*), and of filter-feeding species used for aquaculture such as mussels and oysters suggest that these landing series are indicators of eutrophication. Sponges, red corals, and palinurids, typical of clean oceanic environments, have declined. Overexploitation has become more accentuated in recent years in the Mediterranean, as suggested by the short-term downward trends shown by nine of 27 shellfish species with long-term rising trends and eight of 12 species with long-term declining trends. Of particular concern should be the coincidence of long-term and recent downward trends.

This categorization suggests that a bottom-up effect applies for Mediterranean fauna, namely, an increase in nutrient inputs to a once nutrient-limited inland sea with a very low flushing rate. Invertebrate landing series as a group do not show a completely different range of dynamics from finfish, which presumably reflects similar environmental and fishery impacts and management requirements, although species characteristic of different biotypes can show wide divergences. Evidently, landing trends may be useful indicators of ecological change in specific biotopes.

Monitoring spawning stock biomass and using SRRs or percent spawner-per-recruit models?

Indicator series derived from retrospective analysis and annual biomass surveys are often used to fit SRRs for well-studied Northern Hemisphere fish stocks, but these data sets are rarely available for invertebrates (Caddy 1986*b*). Recent metaanalyses for finfish (e.g., Myers et al. 1994) show that it is no longer safe to assume that spawning populations can be reduced by more than 60–70%, and even these figures may be dangerously optimistic (Caddy and Agnew 2004). Walters and Kitchell (2001) suggested that finfish stock abundance should not fall below 50% unfished spawning biomass, and similar conclusions were reached for abalone by Shepherd and Baker (1998) and for some crustacean resources by Orensanz et al. (1978). For spatially structured populations of sedentary species, SRRs may depend more on local densities than on absolute stock size (Hancock 1973; Orensanz et al. 1998; Orensanz and Jamieson 1998). It has even been argued that a deterministic SRR is not applicable to invertebrate stocks with high fecundity and high density-dependent mortality during their early life history. More recent finfish practice has been to consider the degree of compensation shown by the curvature of the SRR (Iles and Beverton 2000),

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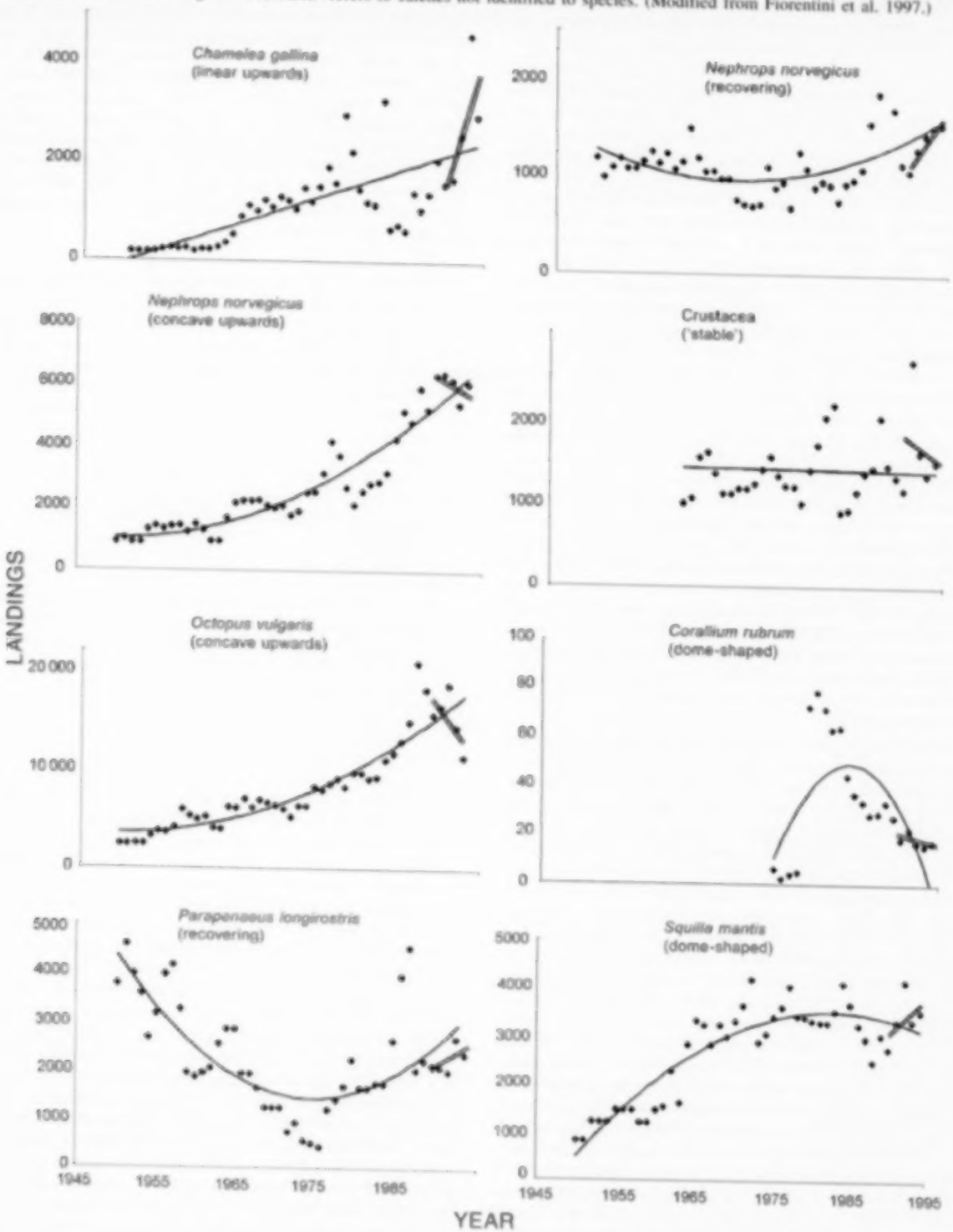
Fig. 4. Some long-term (single line) and short-term (double line) 5-year recent trends for Mediterranean invertebrate landings classified according to the criteria in Fig. 3. "Crustacea" refers to catches not identified to species. (Modified from Fiorentini et al. 1997.)



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and at least for abalone (Shepherd et al. 2001), SRRs are flat and the possibility of depensation (see Liermann and Hilborn 2001) is suggested by the failure of depleted abalone grounds to recover after 15–20 years.

Percent spawner-per-recruit (%SPR) theory (Gabriel et al. 1989) requires that successive generations produce sufficient "spawning units per recruit" (expressed in biomass or eggs) over their life span to replace themselves. Obviously, this is not easy to estimate, nor is it an absolute criterion. If regime shifts reduce productivity, recruitment may decline, and hence, some experts prefer to calculate the actual number of eggs produced by the population. Deriving RPs from %SPR calculations is widely used in finfish management (see ICES 1993; Mace and Sissenwine 1993; Mace 1994). Rates of fishing on abalones that do not reduce spawning potential to below 50% of unfished levels ($F_{50\%}$) were believed appropriate for small stocks and $F_{40\%}$ for large stocks of abalone (Shepherd and Baker 1998). A safe limit of 30% virgin population fecundity was estimated for *Haliotis rubra* by Sanders and Beinssen (1998), below which simulations showed that stock recovery could not be assured. Species such as squids with annual life histories may also require high thresholds (e.g., Agnew et al. 1998). In contrast, conventional wisdom is that high-fecundity spawners such as many sessile molluscs may recover from low thresholds, but even for these, evidence suggests that recruitment is enhanced by healthy source populations. Threshold values of $F_{10\%}$ have been suggested for *Homarus americanus*, whereas the overfishing definition suggested for *Panulirus argus* by the National Marine Fishery Service is triggered when the egg-to-recruit ratio is 5% of the unfished population and recruitment has been falling for 3 consecutive years (Rosenberg et al. 1994). In all cases, calculating an indicator based on relative fecundity of the current to unexploited conditions seems a feasible approach.

A range of "guesses" as to the limiting spawning potential of invertebrates are given (Fig. 5), also incorporating values for pelagic and demersal finfishes for comparison. Like vertebrates, invertebrate species span a wide range of relative fecundities from which populations are believed to be recoverable, but Fig. 4 contradicts the common assumption that invertebrates will always recover from low stock sizes. Whether a scallop population could consistently recover from 2% of the virgin stock size as tabulated by Mace and Sissenwine (1993) probably depends on local density and the degree of aggregation of the remaining spawners as well as on environmental conditions (Haywood and Staples 1993) and not just on total stock size, and the degree of compensation possible after stock depletion may vary significantly (Fig. 5). With few exceptions (e.g., Ennis and Fogarty (1997) for *H. americanus* and Shepherd and Baker (1998) for *Haliotis laevigata*), SRRs have rarely been derived for invertebrates. Effects of environment are often more convincing than the effect of spawning stock size on invertebrate recruitment, and for bivalves, local adult biomass may inversely affect local settlement success (Hancock 1973). The derivation of model-based RPs for invertebrates could follow %SPR or fecundity-per-recruit approaches, but as noted, for sedentary species, local density and location rather than just population size are probably the key variables. Some reservations nonetheless have been expressed concerning the use of %SPR and fecundity-per-recruit measures for lobsters and other long-lived species, as the calculated fecundity of unexploited stocks used for reference in egg-per-recruit calculations requires assumptions as to M values at age, moult frequency, and the mating success for very large lobsters, values that it is rarely possible to verify. It would be more convincing to use indicators comparing fished populations with those in unfished marine protected areas (MPAs). The importance of older lobsters in reproduction has been stressed (Caddy 2002) as for finfish (Conover and Munch 2002), and an indicator estimating mean age or size of mature females could be useful to measure truncation of mature age groups.

Indicators and RPs based on spatial and habitat factors

The term "productive capacity" (Jones et al. 1996) is commonly used to describe "both the carrying capacity of an environment, including the productivity of organisms on which *the species* depends". Indicators reflecting production per habitat area or carrying capacity are especially relevant for invertebrates (e.g., Bolonga and Steneck 1993; Herrenkind et al. 1997) and are critical for sedentary species. Density emerges as a key variable, and Botsford et al. (1993) noted that below 1 female·m^{-2}, successful fertilization of *Strongylocentrotus franciscanus* is limited, and minimum densities for successful fertilization must apply to most sedentary species. Shellfish populations often show contagious distributions such that much of the stock lies within a small proportion of the stock area, which in addition to being the "source" of new recruits is also the most profitably fished component. Indicators of growth rate and mortality should ideally be quantified through time (i.e., under different densities) and in space (by fishing ground) to evaluate variations in density-dependent processes and habitat quality.

The issue of source and sink populations is often referred to for sessile and semisessile invertebrates. For example, the role of source populations for the Georges Bank scallop (*Placopecten magellanicus*) stock was commented on by McGarvey et al. (1992) who found that 82% of egg production came from a small area of the bank and was produced there at a high density. This argument was also invoked for a crustacean, *P. argus*, by Lipcius et al. (1997). The suggestion was made (Caddy 1989) that range extensions during favourable regimes may be extensions of impermanent "sink" fringes. Thus, estimates of range represent expansions and contractions of populations and are useful indicators of productivity (see Caddy and Defeo (2003) for an example on surf clams). It is also suggested that indicator values for density and biomass be collected where possible from source populations.

For invertebrates where metapopulations are the rule (i.e., individual shellfish beds within a fishing area), the concept of a unit stock seems to break down, and even if genetically homogenous, not all segments of the metapopulation are of equivalent value from a population perspective. Mesoscale (local populations) and macroscale or megascale (geographic) patterns are usually present, and some grounds with regular recruitment have a higher probability of sustainable yield and may form "source" populations for adjacent areas (Caddy and Defeo 2003). Especially for sedentary invertebrates, it is important to distinguish between source populations that produce most of the progeny and "sink" areas that

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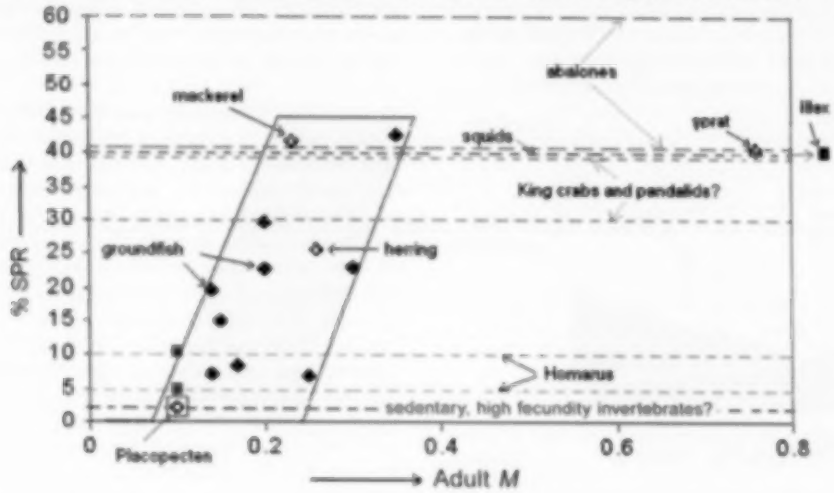
Fig. 5. Postulated ranges of minimum values for percent spawner-per-recruit (%SPR) for fish and invertebrates from which stock recovery is believed possible. Data for a range of finfish %SPRs (most commercial finfish appear to fall within the parallelogram) are from Mace and Sissenwine (1993) and are plotted against natural mortality (M) rates mainly from FISHBASE.



in good years may receive "vagrant" juveniles, as local populations may not be self-perpetuating even though they form part of a metapopulation with a common gene pool (see Orensanz and Jamieson (1998) for a discussion of spatial factors in shellfish populations). If these two groups could be distinguished, it would be legitimate to harvest sink areas without major control as long as the "mother lode" of spawners in the "source" area is protected. It may even be a viable strategy to build up spawner density there, as for many bivalves, echinoderms, and abalones, gamete fertilization is distance constrained, or as for abalone, juvenile dispersal may remain local to the parent population (Shepherd et al. 2001). One criterion for recognizing source areas is to regularly map recruitment areas and protect those where a more even distribution of age classes occurs.

For macrocrustaceans, nursery and spawning areas and migration routes need to be distinguished in management, and serial depletion of crustacean populations was documented by Orensanz et al. (1998) and seems to reflect spatial vulnerability of source areas for these species. An important survey-based indicator, then, is the proportion of the stock area containing densities over some limiting value. Appropriate scales of sampling must be used to characterize the large variation in dispersal dynamics over space and time and the between-site variation in settlement dynamics of larvae. Single "snapshot" studies generally lead to erroneous conclusions; hence, the need to construct indicator series from repeated observations. Life histories and the characteristics of habitat or substrate may cause recruitment bottlenecks and density-dependent processes (Wahle and Steneck 1991). If estimating fishing mortality rate is a problem, as for many semisedentary species, a spatial exploitation strategy could be the solution. Should yield-per-recruit suggest an optimum target F, it may be possible to approximate this by a rotating harvest scheme (e.g., Caddy and Seijo 1999) (see Fig. 6).

Even for motile invertebrates, indicators monitoring nursery areas such as described for *H. americanus* (Wahle and Steneck 1991), *Panulirus* (Acosta and Butler 1997), egg brooding areas for *Cancer magister* (Scheding et al. 2001), and nesting areas (*Octopus vulgaris*) may require special protection and monitoring. Such areas of critical habitat may be more constraining on the effective level of recruitment than trophic considerations and, in some circumstances, perhaps even than minimum spawning stock size. In fact, once a bottleneck is passed in the life history, food and living space may not be the critical constraints (Fig. 7). This suggests that stock enhancement by increasing egg production may not always be the priority, but protecting or enhancing nursery area may be. Mapping and geographic information

Fig. 6. A rotating harvest scheme in which a nonmigratory stock is divided into subareas with approximately equal proportions of stock in each area. The number of areas is equal to, or a multiple of, the rotation period. Variable harvesting rates (60–90%) in the open area by the end of the season are calculated to result in a given F-based target reference point (TRP) = 0.2. Curved lines from top down represent 90% (○), 80% (■), 70% (▲), and 60% (×) of stock harvested in the open area during a year. (From Caddy and Seijo 1999.)

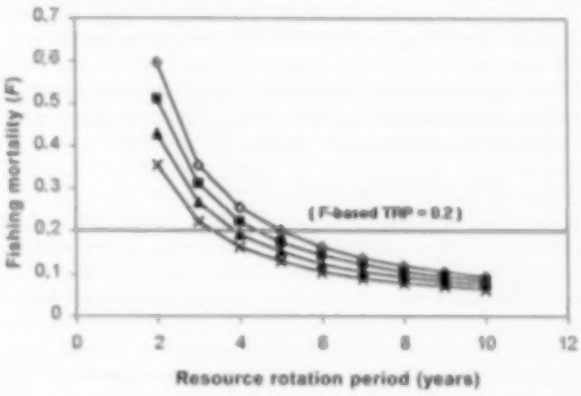


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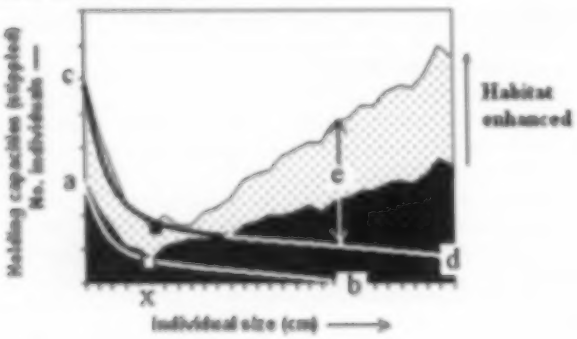
Fig. 7. Illustration that a typical survival curve (*a–b*) will limit survival of adults to below the carrying capacity of the habitat if limited habitat forms a bottleneck at critical juvenile size *X*. Although enhancing habitat holding should improve survival (*a–b* improving to *c–d*), the holding capacity of juvenile habitat is critical, and much suitable adult habitat (*e*) will likely remain unused. Thus, indicators of suitable habitat size could usefully focus on juvenile stages.



systems applied to monitoring critical habitats, their area, and (or) the densities within them are likely to provide fishery indicators with high predictive significance if aggregations of juveniles or spawners occur. The use of overlays to determine degree of interaction between ecosystem components is also potentially a source of useful spatial indicators (e.g., Nishida and Booth 2001).

Measures of year-class regularity

Alternative control laws have been based on an indicator monitoring the proportion of the biomass consisting of older animals. Rosenberg and Brault (1991) suggested such a simple measure of year-class regularity based on the skewness of the age distribution, noting that as exploitation increases, the age composition becomes more skewed, as the population consists of fewer year classes. They defined

$$\text{Skew} = (1/N)\sum[\ (X_i - X_{bar})/s]^3$$

where N is the number of age groups, X_i for $X_1,\ldots, X_n$ is the relative abundance of the ith age group, X_{bar} is the average relative abundance, and s is the standard deviation of the relative abundance. The skewness relative to a value calculated for the unexploited stock might be a useful criterion for judging the success of recovery strategies, i.e., aiming for a given relative skewness as a criterion for rebuilding. The skewness of local age compositions could also be a spatial criterion for distinguishing "source" areas with regular recruitment from "sinks" with only occasional year classes.

The problem of deciding on a common management framework for metapopulations arises frequently for spatially differentiated invertebrate stocks, and Maritime Canada lobster districts, for example, may or may not correspond to separate stocks, and different local management approaches have evolved. Reflecting the fact that few adult lobsters survive to reproduce, a common metapopulation criterion was proposed by the Fisheries Resource Conservation Council (FRCC), namely to increase egg-per-recruit by a uniform 1% in all lobster management districts while allowing some leeway as to how this might be accomplished locally. Thus, individual areas may have a first tier of management measures representing local stakeholder preference where monitoring requirements can vary, but a common element for the supposed metapopulation may be a fisheries control law requiring an overall increase in egg production to be satisfied.

Productivity indicators and their RPs

Indicators and RPs used for finfish management are usually restricted to catch, biomass, and fishing mortality. This may partly explain the poor performance of harvest rules based on limited data inputs in the face of ecological change and regime shifts. A wider range of variables appears to be required for monitoring and managing invertebrate fisheries, and indicators of fishery productivity seem a key option to consider. FAO (2001) defined productivity as "a complex function of fecundity, growth rates, natural mortality, age at maturity and longevity", and productivity seems a reliable surrogate for population resilience. More productive (short-lived) *r*-selected species have high fecundity and growth rates and a rapid turnover of generations and from low numbers can rapidly take advantage of conditions suitable for re-establishment; *K*-selected species with low productivity tend to spend longer periods at low population size once depleted and run greater risk of extinction from depensatory factors. FAO (2001) considered that "the most important property of species and populations relative to risk of extinction is their resilience and ... this is best reflected by the productivity of the species".

Mohn (2002) remarked that productivity is given insufficient emphasis in standard stock assessment, and in fact, a built-in "equilibrium assumption" often seems to rely on recruitment and surplus production being constant, and noted that productivity can also be expressed in terms of the age-specific rates of growth (g), natural deaths (m), fishing (f), and recruitment (R), so we might write

$$B_{t+1} = B_t \exp(g - m - f) + R_t$$

where year-specific subscripts for growth and natural and fishing mortality rates are omitted for convenience, although rates may change from year to year because of changes in environment, food availability, and predator abundance. This equation is not easily solved but suggests that a "characteristic" measuring stock productivity should incorporate indicators reflecting changes in biomass, recruitment, and fishery yield and also monitor, if possible, changes in natural mortality rate and growth.

Quantifying productivity is difficult, but Table 2, based on FAO (2001) and criteria proposed by Musick (1999), suggest a functional classification into three production categories that could also be adopted for invertebrates. Although the International Union for Conservation of Nature guidelines based on small population size may only apply to sessile, semisessile, and extremely low productivity species, where a bottleneck exists at some point in the life history, critical habitat area for some life history stage can be important (Fig. 6). This would be the case if a species passes its (early) life history in a restricted or fragile habitat, such as estuaries, grass beds, or mangrove swamps, where changes in area and density could be indicators of potential productivity. For

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Table 2. Guidelines proposed by Musick (1999) and FAO (2001) for classifying finfish species by productivity (estimates in parentheses from Musick 1999).

Parameter	Low productivity	Medium productivity	High productivity
M (natural mortality rate)	<0.20	0.20–0.50	>0.50
r (intrinsic rate of increase) (year^{-1})	<0.14 (0.05–0.15)	0.14–0.35 (0.16–0.50)	>0.35 (>0.50)
k (von Bertalanffy coefficient)	<0.15 (0.05–0.15)	0.15–0.33 (0.16–0.30)	>0.33 (>0.30)
t_m (age at maturity) (years)	>8.0 (5–10)	3.3–8.0 (2–4)	<3.3 (<1)
T_{max} (maximum age) (years)	(11–30)	(4–10)	(1–3)
Finfish species	Orange roughy, sharks	Cod, hake, plaice	Sardines, anchovies
Possible invertebrate examples	Red coral, abalone, lobsters, Tridacnidae?	Small crabs, *Nephrops*, some pandalids?	Penaeid shrimps, cephalopods

Note: Invertebrates suggested to be added to each category are shown in the last row.

molluscan shellfish, productivity may also depend on environmental inputs such as phytoplankton abundance, seasonal oxygen minima, turbidity, nutrient inputs, etc., and the criteria proposed by Alfsen and Serbo (1993) are relevant here. The critical importance of density as an indicator affecting growth rate, natural mortality (by predation or disease), and spawning success needs to be considered.

Ecosystem and environmental indicators

The existence of "top-down" effects as suggested by Pauly et al. (2001) raises the question of whether top predator abundance is a useful indicator of predatory impact. Invertebrate fisheries where this is apparently the case are interactions of sea otter and abalone (Tegner 1989), northwest African sparids and *Octopus* sp. (Caddy and Rodhouse 1998), gadoids and *Nephrops* in the Irish Sea (Brander and Bennett 1989), and red grouper and *Octopus* sp. (Arreguin-Sanchez 2000). This raises the questions for what species and in what areas and seasons do critical interactions occur and how can they be monitored with meaningful indicators. In the case of gadoids and Norway lobsters (*N. norvegicus*), Brander and Bennett (1989) presented a multispecies bioeconomic yield model that suggested using predator biomass (or perhaps the predator-to-prey ratio) as an indicator in *Nephrops* fishery management. However, Kruse and Zheng (1999) found no obvious correlation between biomasses of groundfish and king crab decline, and Hanson and Lanteigne (2000) reached similar conclusions for cod and lobsters in the southwest Gulf of St. Lawrence. Nonetheless, the conclusion seems inescapable that in some cases, predatory finfish abundance may be a negative indicator for invertebrate fishery productivity. Collie and Gislason (2001) suggested restricting multispecies considerations to the immediate target species and its main predators and prey and considering one-way flows between them, and such empirical indicators are implemented by Link et al. (2002). Thus, predators can be added to single-species prey assessments without considering the totality of ecosystem interactions. The problem of deciding on suitable indicators is, on the one hand, constrained by the usually limited data series available and, on the other, due to the difficulty of deciding on first- and second-order effects of the indicators believed to be relevant (Fig. 1).

The maximum biological production (MBP) is a TRP for productivity that Die and Caddy (1997) showed to be safer than MSY, and for managing prey species, Collie and Gislason (2001) suggested keeping the total mortality rate (Z) below a threshold such that the total allowable catch in year t (TAC_t) is defined by

$$TAC_t = Z_{MBP} B_{av_t} - PC_t$$

where Z_{MBP} is the mortality rate at maximum biological production, B_{av_t} is the projected mean prey biomass in year t, and PC_t is the prey biomass consumed by predators.

The key role of environmental conditions in controlling invertebrate production needs to be recognized in decision-making, as yield largely depends on recruiting year-class size, which for invertebrates is often a function of biotic and abiotic factors but also of anthropogenic effects such as nutrient runoff or incidental impacts of dredging on epifauna (e.g., Pitcher et al. 2000). As highly fecund invertebrates are often low in the food web and sensitive to bottom-up effects, indicators measuring plankton productivity, turbidity, oxygen levels, and eutrophication should be useful in predicting the typically large variations in recruitment success that drive these fisheries.

Indicators derived from biological characteristics

Crustacean biological processes are dominated by moulting, which generally decreases in frequency with age. Hence, a decline in the abundance of older animals with fishing pressure leads to a higher frequency of moulting and a higher proportion of animals in a soft-shell condition, which emerges as an indirect index of exploitation rate (Caddy 1986*a*). The change from juvenile to adult morphological characteristics can also be used as a proxy for age composition, e.g., for conch (*S. gigas*) or whelk (*Buccinum undatum*) populations from the proportion of thick-lipped shells in the catch, as thickening occurs at maturity. Thus, it seems feasible, and probably cost-effective, to develop what may be called "quality indicators" such as sex ratio, annual recruitment, proportion of mature fish in the stock, etc., and measure them by special sampling schemes or from surveys. This type of indicator, coming from an independent sampling from catch rate or fishing effort, should not be subject to the confounding effects that plague production models in which a plot of catch-per-unit-effort against fishing effort compares two variables derived, in part, from the same indicator series.

Fu et al. (2001) investigated the role of sex change in population dynamics and management of a protandrous hermaphrodite, *Pandalus borealis*, in the North Pacific. As

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Table 3. Four possible indicators for each of four characteristics of a traffic light monitoring system for hypothetical crustacean species A with predators 1 and 2 and co-occurring species B.

Indicator	Characteristic
1. Mean survey catch per trap	Abundance
2. Area with density >5·m^{-2}	
3. Early-season catch per trap haul	
4. Bycatch species A in trawl fishery for species B	
1. Number of recruits (carapace length <5 cm)	Production
2. Area of recruit density >10·m^{-2}	
3. Mean size of mature females	
4. Condition factor (carapace length = 10–15 cm)	
1. Mean Z, from survey data	Fishing pressure
2. Fleet days fished per season	
3. Immature individuals (%)	
4. Annual number of trap hauls per area grounds	
1. Abundance (predator1/species A)	Ecosystem/environment
2. Abundance (predator2/species A)	
3. Absolute value [bottom temperature – optimum temperature]	
4. Prey abundance·m^{-2}	

mainly females are exploited, the sex ratio drops with heavy exploitation and impacts reproductive success, and hence, this could be a useful indicator. A related question is raised: what is the optimum age at which to take a cohort of females that is bearing eggs? This has also been a leading question in the Gulf of St. Lawrence lobster fishery. The importance of retaining spawning potential for large fecund crustaceans (for which larger females are less vulnerable to capture) is illustrated by American lobster management in the Maritimes. Some ideas for biologically based RPs for a macrocrustacean are given (Table 3) based on Caddy (2002).

Is there a case for "empirical" RPs?

The examples given earlier illustrate that model-based RPs may be misleading if the model incorporates assumptions at variance with species biology, environmental change (i.e., stability), and demography. Defining RPs using precaution and past experience with the fishery is not excluded in "real-life" management, and for some invertebrates, there are few alternatives to this approach. Conventional fisheries indicators often include fishing intensity (= effort per unit area), with raw data preferably adjusted for fishing power by fleet components. Estimating total catch usually assumes that there is a statistical sampling scheme in place that collates the raw data into an annual figure for each stock unit and that an annual survey programme estimates biomass. Estimates of total catch and fishing effort that depend on sampling the whole fishery or on a census of all fleet operations are particularly liable to bias because of misreporting. Special schemes to sample life history characteristics such as sex ratio, percent soft-shelled animals, etc., may also provide useful and cost-effective indicators.

The use of empirical RPs derived directly from those "historical" values of indicator time series that marked the onset of earlier negative fishery situations is an alternative strategy. Such RPs may also emerge from discussion between experts, managers, and stakeholders. Although less "tidy" scientifically, empirical RPs may represent past unfavourable conditions remembered by stakeholders and thus provide an easily understood incentive to work towards stock reconstruction if this is required.

Although judgement rather than analysis is frowned upon in science, indicators and RPs, strictly speaking, are management tools, and their significance should be understood by stakeholders and interested parties if they are to be effectively used in a management rule. The Law of the Sea and subsequent international legal instruments specify that management action should not be delayed but based on "the best information available" but do not indicate that predigesting fishery indicators through a modelling procedure is mandatory. Rightly or wrongly, judgement on the basis of inadequate data is routinely applied in fisheries management, although it would be greatly improved if formal or informal rules for using information from indicators were incorporated in decision-making. This does not exclude model-based RPs, but some schools of practice use stochastic modelling mainly as a means of testing harvest laws and the (often empirical) RPs that they contain to determine their performance and precautionary nature (e.g., Zheng et al. 1996; Breen et al. 2002) rather than just as a source of RPs.

Use of indicators and RPs in fishery control laws

There are three overall types of control laws driven by stock indicators. (*i*) A constant low total allowable catch (TAC) strategy requires a high escapement and high stock biomass and productivity. Similar strategies are used in New Zealand fisheries, such as the maximum constant yield (Annala 1993) in management of New Zealand rock lobsters. Although constant catch strategies may not be ideal, the difference between total catch and the preset TAC is an essential "response" indicator in quota management. (*ii*) A constant fishing mortality strategy is often considered safer

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for finfish stocks but raises the problem of monitoring fishing power of the fleet having access. This strategy results in a variable spawning stock size and variable catches, especially for stocks with irregular productivity. Sanders and Beinssen (1998) found that the use of TACs to target a fixed exploitation rate is an uncertain method of stock rehabilitation for abalone if recruitment is very variable. Maintaining effort control directly may give more consistent results, but then, increases in fishing power through new technology need to be monitored. Adding a minimum biomass threshold for closure during a low-productivity regime is precautionary so as to avoid overfishing during poor recruitment years even where a cautious (e.g., $F_{0.1}$) strategy is pursued. A ramp function progressively reducing exploitation rate when biomass falls below a precautionary level is the COMFIE approach (ICES 1997). (*iii*) Aiming for fixed escapement to spawning is an option suggested for a prawn fishery (Caputi 1992) and has also been used for short-lived species such as squids (Basson et al. 1996); the Falkland squid fishery (Agnew et al. 1998) targets a fixed escapement to spawning of no less than 40%. This approach requires fishery yield to entirely absorb stock variations from year to year.

Other variants to these three types of control laws are possible, but whatever management regime is in place, a recovery strategy will be called for when stock size falls below an LRP for spawning biomass.

The traffic light approach

The traffic light (TL) system (Caddy 1999*a*, 1999*b*) offers a way of using multiple indicators and their critical RPs for managing populations of invertebrates for which age structure information and SRR-based RPs are unavailable. Initially, a range of indicators measuring quantifiable life history characteristics were envisaged as scored into red or green if they fall on one side or the other of an appropriate LRP. With multiple indicators, the proportion of indicators in the "red" zone might determine the increasing severity of management response. Following intensive consultations (Halliday et al. 2001), the concept was modified to include the use of yellow if indicator values represent an uncertain situation as transitional between a safe or "green" condition of an indicator and "red" indicator values, representing a dangerous condition for the stock. Various approaches were explored for dealing with transitional and boundary situations involving fuzzy logic, ramp functions, etc. The problem that emerges is not just how to define RPs (or in TL terminology, colour boundary values) but, when using multiple indicators, how to weight them before combining them within a "characteristic" for (say) biomass or fishing mortality. No general rules can be offered at this point, but the advantages of working with multiple indicators is evident even if the TL approach is simply providing a diagnostic or index of "ecosystem health", as in impact assessment. Koeller et al. (2000) used this approach for characterising shrimp fisheries, and Halliday et al. (2001) suggested that we refer to this diagnostic tool as a "traffic light stock status index". Combining multiple indicators within a formal management rule is a more complex issue, and the key objective of the TL system is that it should be integrated into a precautionary harvest law, or at least a management information system involving scientists, managers, and stakeholders. One approach proposed by Halliday et al. (2001) is that decision rules should be based on the integrated score of indicator values measuring at least three characteristics: abundance, production, and fishing mortality. Because colour boundaries of individual indicators of a characteristic (e.g., see Table 3) may not be triggered simultaneously, a gradation of response is likely to result, which should provide some redundancy and "smoothing" if the proportion of indicators triggered within a management rule determines the severity of management response (Caddy 1999*a*, 1999*b*).

Other performance measures could be included in a multi-indicator fisheries monitoring system; for example, indicators should ideally monitor key socioeconomic criteria, fleet capacity, and the efficiency of control and surveillance measures (e.g., Fig. 1), with centres of responsibility operating within a fishery management framework monitoring these different indicators as performance measures.

Halliday et al. (2001) suggested that fisheries productivity be given high prominence as it drives fisheries yield and proposed tying this TL diagnostic function to a quota rule. Separate indicator values for productivity, biomass, and fishing mortality could perhaps drive a fuzzy logic decision framework. Some excerpts from a set of quota change rules tied to a TL system might include the following:

IF Production = green AND Fishing mortality = green AND Stock = green THEN TAC increment can be "small positive" BUT:

IF Production = green AND Fishing mortality = yellow AND Stock = yellow THEN TAC increment is "no change" OR:

IF Production = yellow AND stock = red THEN TAC increment must be "large negative".

Changes in the coming year's TAC would thus be determined by changes in three sets of characteristics and their respective indicator values. The resulting quota changes relative to last year's allowable catch would be dictated by precautionary rules: favourable conditions allowing a small increase in quota but unfavourable changes resulting in a larger cut, the opposite tendency to that often produced by conventional management in the absence of capacity control, which tends to result in continual increases in exploitation pressure. An alternative approach suggested informally by the FRCC is to tie the TL diagnostic to a "consideration matrix". This requires scientific advisors to place the current fishery within one of a number of cells in the matrix, each corresponding to a combination of stock condition and productivity regime. The managers must then operate within the constraints for allowable quota change prespecified within each "box". Although the scientific component and multi-indicator approach with these types of strategy appear less precise than when quota management is driven by formal assessments or other population analytical tools, the procedure emphasizes that the most important contribution to the rigor of a management rule comes when decision rules seriously constrain management choices.

A similar system of multiple indicators was the "trouble spot thermostat" proposed by Shepherd et al. (2001) for an

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abalone fishery, which is a good example of using multiple indicators in a harvest law for the data-poor shellfishing grounds making up a metapopulation. This protocol for managing individual fishing grounds of greenlip abalone uses diver survey, and analysis of commercial shell samples allows a response to declines of local populations. Recruitment time series emerged as sensitive indicators, as did the total catch from, and degree of spatial contraction of, individual subpopulations. Catch-per-unit-effort, size frequency, and total mortality (Z) proved to be relatively insensitive indicators of population decline.

Indicators and RPs within stock rebuilding strategies

High-value stocks, as for many invertebrates, are eventually fished down unless an appropriate management framework is in place. Perry et al. (1999) postulated three phases in scientific information gathering in support of management: (*i*) collecting and synthesizing existing information, (*ii*) collecting new information and evaluating alternative management strategies, and (*iii*) monitoring commercial fishing while the chosen management actions are implemented. Less optimistically, given extensive experience with South American shellfisheries, Castilla and Defeo (2001) suggested that development of shellfish fisheries tends to follow six phases: (1) initial exploitation phase, (2) expansive extraction phase, (3) overexploitation phase, (4) closure phase, (5) stabilization of extraction and institutionalization phase, and (6) mature and consolidation phase.

Planning a formal management approach for many fisheries often awaits phase 3 or even phase 6, and initiating a recovery plan in phase 6 requires a lower, sustainable level of exploitation by a limited number of stakeholders with, by now, rights-based approaches such as individual transferable quotas. All phases need indicators to be monitored, but recovery simulations require an approach to the use of RPs that differs from "business as usual" management but must be understandable to stakeholders. The end point for a stock recovery plan is a TRP (e.g., B_{MSY}), expressed in spawning biomass. This should be higher than the LRP infringed in the stock decline; otherwise, the fishery will simply oscillate around this unsatisfactory level once recovery has been achieved (Caddy and Agnew 2004). During stock rebuilding, sequential targets expressed in terms of biomass- and F-based TRPs should dictate a recovery trajectory and attempts should be made by sampling and surveys to determine the probability that this is being maintained. It is now common practice to simulate the fishery as a way of testing recovery strategies before application, but unlike MacCall (2002), most recovery plans assume that the fishery is the key controlling factor, and rarely is specific account taken of regime shifts or ecosystem changes that may contribute to stock collapses; hence, unrealistically short recovery times may be predicted. Five phases can be recognized in a rebuilding plan: (*i*) the (spawning) stock biomass indicators drop below LRPs established previously during routine exploitation, and this initiates the recovery plan (already prenegotiated with stakeholders), (*ii*) a recovery trajectory is defined as a series of (preferably) time-specific TRPs for fishing mortality and biomass (although the recovery trajectory may be accelerated or slowed depending on recruitment), (*iii*) a recovery TRP for biomass is defined, which when reached will terminate the recovery plan, (*iv*) when the biomass indicator is back above the recovery TRP, optimal harvesting may resume at levels applied before collapse, but a more precautionary approach would carry forward aspects of the recovery plan, for example, the use of multiindicator monitoring of productivity, and (*v*) indicators and their RPs should be incorporated into the legislative framework for the fishery.

Apart from slow-growing species, those with low larval dispersal and (or) species with restricted or vulnerable habitats such as the Tridacnidae, pearl oysters, *Pinna* spp., and holothurians, stock rebuilding has not been the major problem for most invertebrates that it has been for marine fishes. Despite this, a significant number of invertebrates and their local stocks may be in danger of extinction (see Wells 1989). Rebuilding approaches have tended to focus on closures (see Castilla and Defeo 2001), although for some invertebrate stocks, stock building seems more a consequence of the collapse of predatory fish populations than of a deliberate building plan (Caddy and Agnew 2004).

Discussion

The transition from dominance by TRPs as implied by the Law of the Sea to precautionary LRPs as recommended following the United Nations Conference on Environment and Development and the 1995 United Nations Fish Stock Agreement has led to a focus, at least in finfish science, on RPs generated from fisheries models. This requires judgement as to the applicability of a model, and some examples are given of potential errors resulting from uncritical use of "generic" as opposed to specific models fitted to indicator series and used to generate RPs. The role of judgement, by either scientists, managers, or stakeholders, in deciding on RP values and agreeing on them with stakeholders is essential to a precautionary management framework that will be respected in practice. Given the usual inadequate data and research backing, empirical RPs based on "best available evidence" whether historical or biologically based cannot be excluded from use.

Practical experience with the formal use of multiple indicators in fisheries management for finfish or invertebrates is still limited, but the importance of monitoring a range of ecosystem and fishery characteristics and the need for further advances in this area are highlighted. Achieving a degree of redundancy by the use of multiple indices may help avoid errors resulting from basing decisions on only one or two indicator series. The systematic use of indicators has been approached here from the perspective of their incorporation in a decision-making framework. Two approaches are mentioned: the various (D)PS(I)R frameworks and the TL approach. Both can be used simply for monitoring or can be incorporated into fisheries control laws as functional components of the fisheries management cycle. The low precision possible in most fisheries information gathering structures calls for the definition of ranges of indicators corresponding to safe, uncertain, and unsafe conditions, and the colour convention used in the TL approach to management makes it clear that if indicator variance is high, it is not a question of directing the fishery onto "optimal points" as defined by a

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TRP but of avoiding dangerous or uncertain zones, which are always likely to be poorly defined.

The growing concern with ecosystem management of fisheries resources requires that monitoring also be focussed on likely interactions with other members of the ecosystem. Notable here might be key predator and prey species, competitors, parasites, and biotic habitat components providing cover or settlement surfaces. Impacts of changes in environment affecting recruitment and bottom-up effects will need to be distinguished by the use of appropriate indicators from top-down effects. Environmental, abiotic, and biotic factors have important implications for fishery management policy, especially with regard to stock recovery, and as an integrated ecological approach to monitoring for all resources is required, this may be achieved in a cost-effective manner.

Recent experience with recovery of depleted fish stocks suggests that specifically defined fishery recovery plans will require backing from an appropriate information gathering function, with nondiscretionary management actions taken when indicators approach values preagreed to with stakeholders. These RPs, and the mandatory responses that they trigger, need to be incorporated into an overriding legislation. Work to date on stock recovery suggests that concentrating on two or very few indices such as fishing mortality and (spawning) biomass is not likely to adequately track stock recovery if regime and ecosystem changes are underway. The use of indices of productivity and, for semisessile or sessile invertebrates, indicators monitoring local density within metapopulations will be necessary.

Examples are given of how the apparently less precise or quantitative approaches discussed here may be incorporated into a system of management rules that constrains possible management choices. Combining a monitoring system of multiple indicators with a response or quota change rule, such as the consideration matrix of the FRCC, or logical statements based on indicator values, as suggested by Shepherd et al. (2001) and Halliday et al. (2001), ensures that precautionary considerations are incorporated into management decision-making. This approach can be criticized because it is less "scientific", but it nonetheless offers the potential of maintaining the fishery ecosystem within a sustainable range of conditions, is easily understandable to stakeholders, and can be extended to monitor socioeconomic performance and other issues of concern to the fishing industry.

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PERSPECTIVE / PERSPECTIVE

Biological reference points in the management of North American sea urchin fisheries[1]

Louis W. Botsford, Alan Campbell, and Robert Miller

Abstract: The precautionary approach calls for both target and limit reference points (TRPs and LRPs, respectively) and notes the vulnerability of developing fisheries to excess effort. LRPs should reflect a population's ability to continue to persist, which depends on lifetime egg production (LEP) and current abundance. The unique characteristics of sea urchin fisheries, such as (*i*) tight ecological coupling, (*ii*) their being roe fisheries, (*iii*) protection of juveniles under adult spine canopies, and (*iv*) broadcast spawning, can influence their management. Most North American sea urchin fisheries developed rapidly. Their reference points include (*i*) several LRPs and TRPs based on the logistic or surplus production model, (*ii*) a unique TRP involving direct monitoring of the bathymetric position of their macrophyte food, and (*iii*) an LRP based on the fraction of natural, unfished LEP. The dominant effect of fishing down and serial depletion on catch and effort data from developing sea urchin fisheries adversely affects fits to the logistic model. Reference points based on tight ecological coupling will be useful only where food webs are simple and one-dimensional. Sea urchin fisheries developed in the future should consider the fraction of natural LEP as an LRP and attempt to limit early excess fishing capacity.

Résumé : Dans les pêches commerciales en développement, le principe de précaution exige l'élaboration de points de référence cibles (TRP) et de points de référence limites (LRP) et il souligne la vulnérabilité de telles pêches aux efforts de capture excessifs. Les LRP devraient représenter la capacité de durabilité de l'espèce qui dépend de la production d'oeufs au cours de la vie (LEP) et de l'abondance actuelle. La gestion de la pêche aux oursins de mer doit tenir compte de caractéristiques particulières, par exemple (*i*) il existe un couplage écologique serré, (*ii*) ce sont les oeufs qui sont récoltés, (*iii*) la protection des petits se fait sous un couvert formé par les épines des adultes et (*iv*) les gamètes sont libérés à grande échelle au hasard. La plupart des pêches commerciales d'oursins en Amérique du Nord se sont développées rapidement. Leurs points de référence incluent (*i*) plusieurs LRP et TRP basés sur le modèle logistique ou de production excédentaire, (*ii*) un TRP particulier impliquant l'évaluation suivie et directe de la répartition bathymétrique des macrophytes qui servent de nourriture aux oursins et (*iii*) un LRP basé sur la fraction de LEP naturel et non récolté. L'effet principal de la pêche excessive et de l'épuisement continu sur les données de capture et d'effort de pêche dans une pêche commerciale d'oursin en développement est de diminuer l'ajustement au modèle logistique. Les points de référence basés sur le couplage écologique serré ne seront utiles que là où les réseaux alimentaires sont simples et unidimensionnels. Dans les pêches d'oursins qui se développeront à l'avenir, on devrait considérer la fraction de LEP naturel comme un LRP et essayer au début de limiter la capacité de pêche excessive.

[Traduit par la Rédaction]

Introduction

Recent history clearly indicates that sea urchin fisheries are in need of better management worldwide (Andrew et al. 2002). Although sea urchins have long been enjoyed by many cultures around the world, recent increasing demand in the Japanese market and a shift in the exchange rate of the yen have driven rapid development of new fisheries, as well as expansion of old ones, for export (Fig. 1). World catch was dominated by Japan in the 1960s, with fisheries in Chile, southern California, and Mexico developing in the 1970s. The dramatic increase in the mid-1980s with the change in

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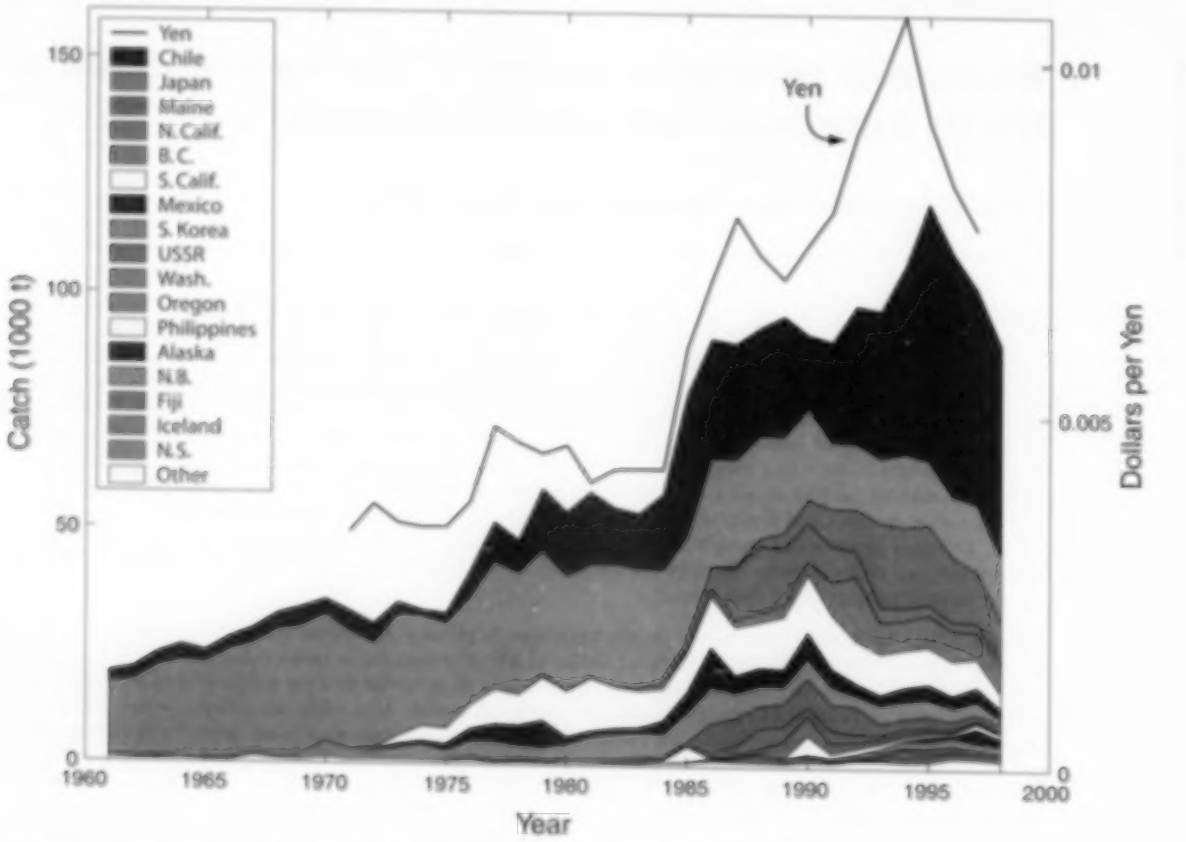
Fig. 1. Global sea urchin landings plotted cumulatively to display the contributions of North American landings and the transient nature of recently developed fisheries. The variation in the dollar value of the yen is also shown. B.C., British Columbia; Calif., California; N.B., New Brunswick; N.S., Nova Scotia; t, tonnes.



value of the yen was primarily due to the development of new fisheries, many of which declined after 5–10 years (e.g., northern California, Maine, Washington, and Oregon). Rapid development or expansion of fisheries usually takes place with a minimal amount of data and analysis for management, yet it is a critical stage of a fishery (Perry et al. 1999). In addition to this recent increase in pressure on sea urchin fisheries, their exploitation is confounded by some of their unique population characteristics (Lawrence 2001).

Here, we review the management of sea urchins, with emphasis on North America and a quantitative focus on the population dynamic basis for management decisions. We assess the various approaches to management in the context of biological reference points as used in the precautionary approach to fisheries management. The precautionary approach to fishery management includes a number of devices for addressing and reducing the effects of uncertainty so that fisheries can be operated in a way that is sustainable in spite of the inherent uncertainty (e.g., Caddy and Mahon 1995; Food and Agriculture Organization of the United Nations 1995). One of these is the definition of reference points, a target reference point (TRP) and a limit reference point (LRP). It also calls for special caution in the case of developing fisheries, a call that has not been heeded in the recent rapid development of sea urchin fisheries (Fig. 1). The federal fishery agencies of both Canada and the United States have adopted elements of the precautionary approach, and in particular TRPs and LRPs (Restrepo et al. 1998; Shelton and Rice 2002).

Population persistence

Although TRPs can reflect a variety of desired biological or economic goals, LRPs by definition will be most effective if they reflect a population's current propensity to continue to persist. Because sea urchins are relatively sedentary and distributed over space, and vital rates and fishing mortality can vary over space, we should consider persistence of a metapopulation. Because sea urchins are iteroparous, age structure will be important in the individual subpopulations within that metapopulation, so we should look to the current understanding of the persistence of age-structured models.

Population persistence in virtually all age-structured models, regardless of whether the models include density dependence and environmental variability, depends primarily on population growth rate (λ in discrete time or r in continuous time) or alternatively on the lifetime egg production (LEP) (referred to as R_0 in ecological models). For example, whether the simplest of age-structured populations (no density dependence, no environmental variability) will increase

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depends on R_0 being greater than 1.0. This reflects the fact that for a population to persist, individuals have to reproduce enough in their lifetime to replace themselves. The problem in marine populations is that we do not know the number of eggs in a lifetime required for an individual to replace itself, primarily because estimating the egg-to-recruit relationship involves poorly understood early life history phases. Models that include environmental variability in addition to age structure indicate that there is still a dependence on LEP but that the growth rate is reduced by increasing variability (Tuljapurkar 1990; Cisneros-Mata et al. 1997). Models with environmental variability also indicate that the likelihood of a population collapsing within a certain time frame depends on initial abundance in addition to LEP or growth rate. However, growth rate or LEP has greater primacy because a population with negative growth rate, or a value of LEP below replacement, will always decline, but there is seldom a critical abundance below which collapse is assured.

Age-structured models with density dependence reflect the fact that in unfished populations, LEP is greater than required for persistence (e.g., Botsford and Wickham 1978; Sissenwine and Shepherd 1987; Botsford 1997). The equilibrium level of recruitment is the point at which a straight line through the origin with slope 1/LEP intersects the egg–recruitment relationship (Fig. 2). As LEP is reduced by fishing, egg production and recruitment decline until the population eventually reaches the minimal value of LEP required to persist. Fishery biologists have spent considerable effort to determine this limit, which for the sake of generality is expressed as the fraction of unfished LEP (i.e., the fraction of unfished spawning stock biomass per recruit or eggs per recruit). Early indications were that this limit was near 35% (Clark 1991; Mace and Sissenwine 1993), but the current view is that higher values are required, depending on taxon and environment (Myers et al. 1999, 2002; Clark 2002). The actual value of this parameter is uncertain.

Going beyond single populations to the persistence of metapopulations incurs even greater uncertainty in our understanding of dynamics. In that case, the eggs produced do not just become larvae that return to the same population, but rather, they are dispersed to other subpopulations, which in turn produce offspring that may return to the subpopulation under consideration. Thus, expressing the replacement involved in LEP is even more difficult. When one also considers the fact that dispersal paths are virtually unknown for all marine species other than those dispersing a few hundred metres, this becomes even more uncertain. We are slowly beginning to understand the persistence of these populations, primarily in the context of marine reserves, where we are explicitly interested in persistence of metapopulations in heterogeneous habitats (Botsford et al. 2001; Armsworth 2002; Lockwood et al. 2002). The most important result for our purposes here is that persistence still depends on the critical value of LEP. A subpopulation at any point still needs a certain value of effective LEP to persist; however, the calculation of effective LEP changes to include the spatial configuration of productivity and the destination of the larvae produced.

Because the logistic or surplus production model is often recommended in the management of fisheries with poor data (e.g., Garcia et al. 1989; Caddy 1998; Gabriel and Mace 1999), the question of what that model actually indicates regarding persistence is relevant. Because the logistic model does not explicitly contain commonly observed biological processes such as growth, mortality, and reproduction, it is difficult to relate the persistence conditions for that model to observations of vital rates. Setting the LRP to the maximum sustainable yield (MSY) of the logistic model is conceptually reasonable, but the parameters typically used to specify it are difficult to estimate. In addition, the nonequilibrium mechanisms that are germane to sea urchins (i.e., the fishing down of the size structure and serial depletion) are not contained in the logistic model.

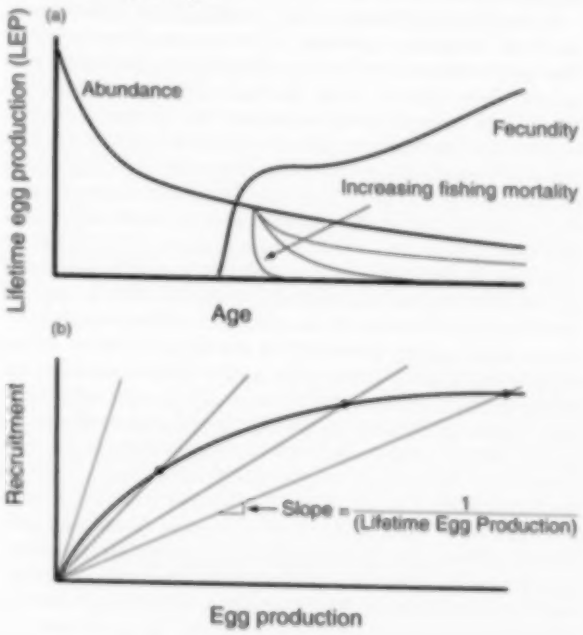

Fig. 2. Graphical view of the factors determining equilibrium population levels in an age-structured model with density-dependent recruitment. (*a*) As fishing mortality increases, there are fewer old individuals. (*b*) This reduces lifetime egg production (LEP), thus changing the equilibrium. With increasing fishing mortality, the equilibrium moves from the natural, unfished value to lower values of egg production. Eventually, 1/LEP becomes greater than the slope at the origin and the equilibrium is zero, indicating collapse.

Special characteristics of sea urchin fisheries

Sea urchin populations share the metapopulation structure common to invertebrates, but in addition, they exhibit several unique characteristics that can affect their management. The first is that tight ecological coupling of the benthic stage of sea urchins to the rest of their ecosystem has been identified. This is due to the "simple" structure of sea urchin food webs involving a single resource, a macrophyte, and one or a few predators, e.g., cunner, ocean pout, and wolf fish on the east coast and sea otters, sheephead, and sea stars on the west coast (Miller 1985; Keats et al. 1987; Jackson et al. 2001) (Fig. 3). Typically, if not controlled by a predator, sea urchins can reduce the algal population to low levels, estab-

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lishing "urchin barrens" of poorly fed sea urchins with little reproduction (Keats et al. 1984).

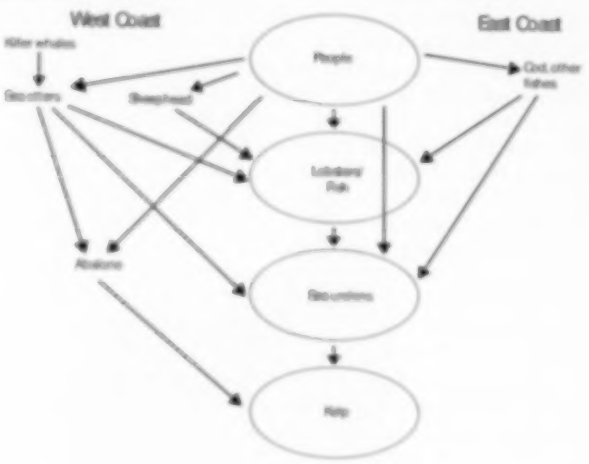
A second unique feature of sea urchin fisheries is that they are "roe" fisheries focused on the male and female gonads. Because production of these is density dependent (Chapman 1981; Levitan 1989) and sea urchin density can be changed dramatically by other species, the fact that sea urchin fisheries are roe fisheries elevates the importance of the tight ecological coupling.

A third unusual feature is the potential Allee effect resulting from broadcast spawning (Levitan and Sewell 1998). This could increase the susceptibility of the fishery to collapse if there were a sharp decline in larval production as density was reduced by fishing rather than a smooth decline to zero. On the positive side, however, this Allee effect is potentially detectable by methods other than reducing a population to low levels by fishing. There have been several direct observations of the effects of spacing between individuals (e.g., Pennington 1985) on fertilization efficiency, and these can be expanded to determine their effects on stock–recruitment relationships (e.g., Claereboudt 1999; Lundquist and Botsford 2004). A relevant recent modeling result indicates that the sharp threshold in the dependence of larval production on adult density that is often envisioned (e.g., as in Quinn et al. 1993; Botsford et al. 1994) will occur only under rather specific, unrealistic biological circumstances. A sharp threshold density, below which there is no larval production, occurs only when the gamete dispersion function has a disc shape (*i.e.*, no dispersion beyond a fixed distance) and individuals have exact regular spacing (Lundquist and Botsford 2004). For biologically more reasonable Gaussian or exponentially shaped dispersion functions and randomly distributed individuals, the dependence of larval production on adult density may still be depensatory, but it will change gradually and differ much less from a linear relationship.

Ebert (1998) proposed that maintaining the fishery above the level of this depensatory mechanism should not be a basis for management, but the mathematical basis for his objection is questionable. It is based on an analysis of the sensitivity of the growth rate of a density-independent population to a change in fecundity, noting that the sensitivity is low in comparison with the sensitivity to survival and growth parameters. However, fishing is not directly changing the reproductive rate of a density-independent population in this case; rather, density dependence is reducing reproduction to a value near zero at nonzero density. The dynamics of a density-dependent population with depensation are quite different from the dynamics of populations without density dependence (e.g., Knowlton 1992).

A fourth special characteristic, present at least in the red sea urchin (*Strongylocentrotus franciscanus*), is the effect of the adult spine canopy in protecting juveniles from predation (Tegner and Dayton 1977). Although this is commonly referred to as an Allee effect, it increases with density linearly from zero, as does egg production. The differences are that it operates after dispersal and is proportional to the sum of individual spine canopy areas rather than individual fecundities. The effect of spine canopy is complicated by the fact that it may add to a fixed amount of juvenile protection supplied naturally by the habitat. The fact that sea urchin spine canopies also protect juveniles of other species, such as abalone (Day and Branch 2002), adds another dimension to the tight coupling with other species.

Fig. 3. Simple trophic structure associated with sea urchins on the west and east coasts of North America. Note that there is some uncertainty in certain historical aspects. (Modified from Jackson et al. 2001.)



World sea urchin fisheries

The management needs for the world's sea urchin fisheries are indicated by the temporal dynamics of global catch records: some declines in long-standing fisheries but a preponderance of recent rapid development and decline of new ones (Fig. 1). The dominant Japanese fishery declined through the 1980s. The large Chilean fishery began to decline in the mid-1990s as the stocks in Region X in southern Chile were completely "fished down" to a recruitment-only state. The trends in these two huge fisheries and a shift in the exchange rate of the Japanese yen drove the development of smaller, more ephemeral fisheries throughout the world. Fairly large fisheries developed in South Korea, Mexico, and southern California in the 1970s, and each has declined slowly with time. In the mid-1980s, large fisheries developed dramatically in northern California and Russia followed by increasing catches in Washington and Oregon. As the initial high catches from those faded, the fisheries in Maine and British Columbia increased in catch and then declined. Fisheries in New Brunswick, Alaska, and Nova Scotia increased in catch in the 1990s.

Thus, global high catches since the mid-1980s have been sustained by a series of transient increases and then declines in different locations. Each developed rapidly with little formal management, at least initially. They typically involved two important transient mechanisms: (*i*) serial depletion on a variety of spatial scales and (*ii*) fishing down of the older, larger individuals that had accumulated over the years. Each of these is a complex, nonequilibrium process that complicates modeling and management. Serial depletion involves movement of fishers to selected areas of high density and profit so that the concentration profiles are reduced essentially by removing the highest first (e.g., Campbell et al. 1998; Orensanz et al. 1998; Prince and Hilborn 1998). Fishing

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down involves removal of all size classes above a limit, which leads eventually to a rather narrow harvested size distribution, just above the size limit. This process is usually not reversed, leading to its characterization as a "one-way trip" (Hilborn and Walters 1992). Neither of these transient effects is accounted for in standard fishery models, and their combination in the same fishery is particularly problematic. Serial depletion and fishing down older larger individuals have played a dominant role in the development of North American sea urchin fisheries.

North American sea urchin fisheries

Alaska

The sea urchin fishery in Alaska sporadically landed both green (*Strongylocentrotus droebachiensis*) and red sea urchins through the 1980s and early1990s but was affected by marketing problems and increasing predation resulting from expansion of the range of sea otters (Andrew et al. 2002). Catches increased to the range of 2000 tonnes (t) in the late 1990s. The fishery is managed on the basis of a total allowable catch (TAC) from the logistic model using current biomass, B, from a triennial survey (Woodby 1998). The TAC = XMB, where the scaling factor X is 0.4, and natural mortality, M, is estimated to be 0.16. There are no size limits.

British Columbia

The red sea urchin dive fishery in British Columbia has experienced two phases: early rapid growth and a period of relatively constant catch. The first phase involved the fishery growing from four vessels landing 75 t in 1978 to 102 vessels landing 12 480 t by 1992. In the second phase, a precautionary approach was initiated in 1993 to avoid overharvesting urchin populations in a data-limited situation (Campbell et al. 1999*a*). Landings were arbitrarily halved to 6106 t in 1993 and controlled thereafter by separate quotas set for the northern and southern coasts of British Columbia.

Current fishery regulations include limited license entry (110), a minimum legal size (100-mm test diameter; note that size limits throughout will be test diameter and will be given in millimetres), and a quota system to provide a conservative fixed exploitation rate of about 2% of estimated biomass. Annual surveys were started in 1993 to determine densities and size frequencies representative of different areas. Quotas or TACs for specific general areas are estimated as XMB_c (using current rather than initial biomass as in Gulland (1977) and Schaeffer (1954)), where X (precautionary scaling factor) is set at 0.2, M (natural mortality) is set as 0.10 (but is provided as a range of 0.05–0.15 to managers), and B_c (current biomass) is calculated as the product of mean (lower 90% confidence limit also provided as a more precautionary alternative) density and mean individual urchin weight of legal-sized urchins and fished bed area. To reduce uncertainty in estimating areas fished, in recent years, fishers have recorded daily fished locations and catch data in logbooks that have been digitized and linked to a geographic information system spatial database (Campbell et al. 2001).

Fishers requested a reduction in the minimum size limit to improve roe quality. Analyses of the dependence on harvest rates and size restrictions of yield-per-recruit (YPR) and eggs-per-recruit (EPR) in simulated red sea urchin populations (Campbell et al. 1999*b*) resulted in a lower size limit of 90 mm accompanied by a 12% reduction in the quota starting in the 2000–2001 fishing season (Campbell et al. 2001). A maximum size limit was considered but not deemed necessary because the low exploitation rate appears to leave sufficient numbers of large urchins to provide spine canopy protection for juvenile survival.

A fishery for green sea urchins in British Columbia began in 1987 (Perry et al. 2001). Catches peaked in 1992 at 1019 t and then declined to a level near 150 t, which they have maintained since 1995. A lower size limit of 55 mm and specified seasons during the peak spawning periods of January–February and October–December were instituted in 1988. The number of licenses has been limited, and an annual TAC has been equally allocated among license holders.

Biological reference points for the British Columbia green sea urchin fishery are based on the logistic model using catch and logbook data required of fishers (Perry et al. 2001). The logistic model was fit using the regression method of Schnute (1977) and the time series method of Pella and Thomlinson (1969). The data used were from 1987–1999, which included the period of early development and associated transient effects (fishing down and serial depletion) not included in the logistic model. These two methods gave similar results. The value of fishing mortality, F, corresponding to MSY was taken to be the LRP and F for the TRP was set at a lower level of (0.25–0.5)MSY.

Washington

The fishery for red sea urchins in the state of Washington began in the 1970s and developed to a peak catch of 4024 t in 1988 and then began to decline. A small fishery for green sea urchins began in 1986. Washington has the only sea urchin fishery that has employed a rotating spatial harvest (RSH). They used a rotational period of 3 years from 1977 to 1995. There were both lower and upper size limits on the fishery, but the upper size limit was not rigorously observed. The green sea urchin fishery was managed on the basis of a size limit and ad hoc annual quotas.

The Washington fishery was analyzed using two different stage-structured models. Pfister and Bradbury (1996) formulated a stage-structured model with three stages: less than legal size, legal size, and greater than legal size. They evaluated a number of harvest schemes with this model, but the results are difficult to interpret, since each stage had a constant "recruitment" each year in addition to the numbers growing into the stage from the next lower stage.

Lai and Bradbury (1998) modified Sullivan et al.'s (1990) catch-at-length model to use survey data rather than sizes of the catch. They fit the growth parameters of that model to 6 years of survey data and then used the resulting parameters describing stochastic growth- and size-dependent natural and fishing mortality to project catches under various fishing mortality rates, size limits, and RSH schemes. They used the maximum equilibrium catch as a biological reference point, which is somewhat unconventional because it depends on the size limit and rotational scheme rather than being a characteristic of the population. They found little improvement in average annual harvest using RSH but that RSH reduced variability in catch.

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Fig. 4. Comparison of size distributions from (*a*) an unharvested and (*b*) a harvested population of red sea urchins from northern California. Estimates of fishing mortality rate require estimation of natural mortality from an unfished population and then use of that value in the fished population (from Smith et al. 1998).

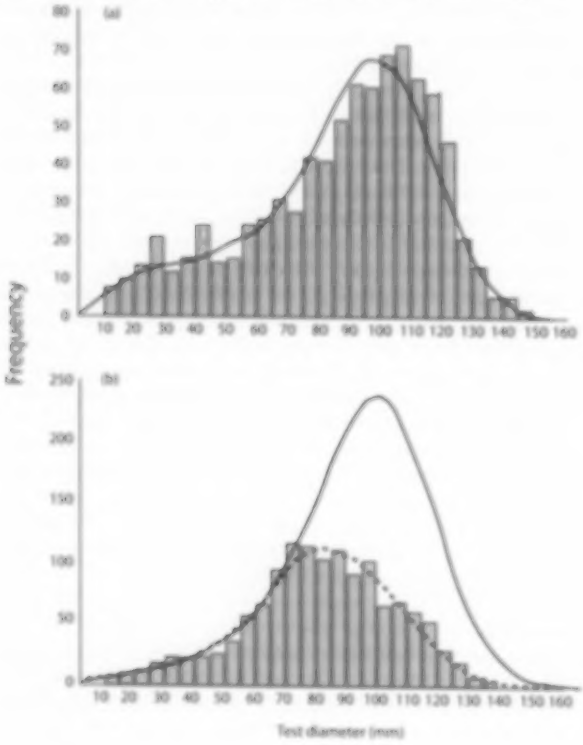
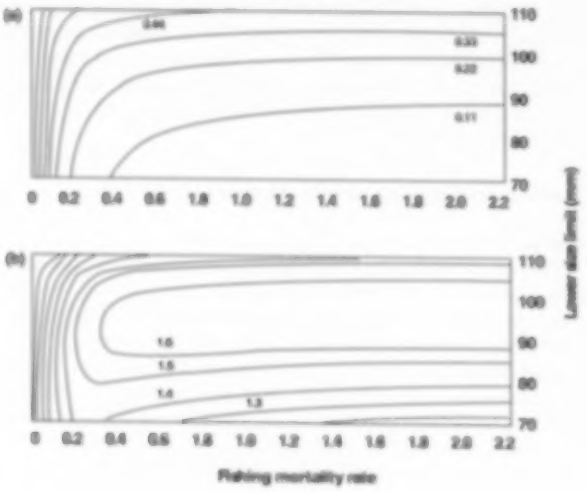


Fig. 5. (*a*) Eggs-per-recruit (EPR) and (*b*) yield-per-recruit (YPR) for red sea urchins in northern California. The current size limit is 89 mm and estimates of fishing mortality rate vary by about 1.0-year^{-1}. (Redrawn from Morgan et al. 1999.)



Oregon

The fishery for red sea urchins in Oregon began in 1986 and peaked at 4220 t in 1990 and then declined steadily (Andrew et al. 2002). The fishery has a size limit of 89 mm. The fishery currently produces about 100 t-year^{-1}.

California

A fishery for red sea urchins began in southern California in the early 1970s and catches rose by 1980 to near 10 000 t. That level was maintained until 1990 when catches and abundance indices began to decline (Kalvass and Hendrix 1997). The fishery expanded to northern California where it increased dramatically in the mid-1980s to 14 000 t and then declined to a level of less than 2000 t where it has remained. In both locations, the spatial focus of effort shifted as different areas were fished down. A moratorium on new permits began in 1987. Size limits of 89 mm were implemented in both locations in 1990–1992. Fishing is restricted in the south to 240 days and in the north to 233 days.

In the northern California fishery, much of the rapid decline in catch was determined to be due to fishing down, although a decline in recruitment was also probably involved. This conclusion was reached by comparing an index of the degree of fishing down, based on samples of the size distribution, with the decline in fishable biomass as evidenced in the trends in catch-per-unit-effort (CPUE) (Botsford et al. 1998). For three out of the four ports examined, CPUE declined more rapidly than the index of fishing down, but this difference was significant only in one of those.

A method for estimating growth and mortality from the data available from sea urchins, size distributions and size increments, was developed in northern California (Smith et al. 1998). The bias and precision of estimates of the mean and variability in L_∞, von Bertalanffy's k, and natural mortality for various values of sample sizes, measurement error, recruitment variability size selectivity and bin sizes were assessed using artificially generated data (Smith et al. 1998). Reasonable estimates of these parameters were possible under most conditions with 200 size measurements and 30 size increments. One characteristic of the estimation that is probably generally true of sea urchin distributions (and possibly those of other invertebrates) is that it was not possible to estimate fishing mortality from a single fished size distribution. Rather, it was necessary to have a size distribution of an unfished population from which to estimate growth parameters and natural mortality before attempting to estimate fishing mortality rate from a fished distribution (Fig. 4).

The estimation method was used to explore potential spatial variability in productivity from size distributions collected along the coast and growth increments from passive integrated transponder tags from several unfished locations (Morgan et al. 2000). Growth and natural mortality were remarkably similar along the coast with an exception at one location. Estimated fishing mortality rates varied in an unexplained way between 0.11 and 1.87-year^{-1} but were for the most part near 1.0-year^{-1}.

These estimates of growth and mortality parameters were used to examine EPR and YPR for northern California (Fig. 5). YPR was generally close to the maximum value for the estimated fishing mortality rate of 1.0 year^{-1}. EPR was low in comparison with accepted values for finfish popula-

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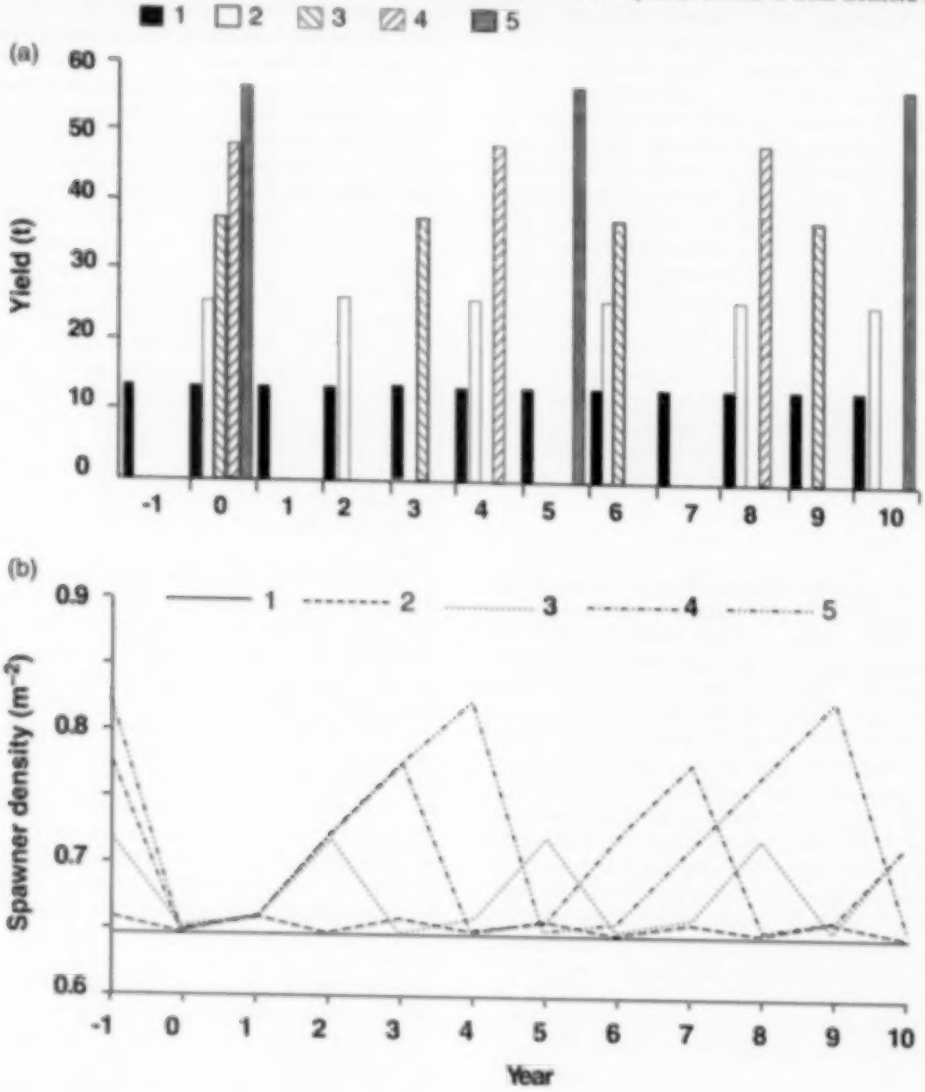
Fig. 6. Results from an analysis of rotating spatial harvest (RSH) with constant recruitment: (*a*) yield versus time for various rotation periods (1–5 years) and (*b*) adult density versus time for various rotation periods (1–5 years). (Redrawn from Botsford et al. 1994.)



tions, about 20% of the unfished level as compared with accepted values of 35–50% for finfish.

Two forms of spatial management were assessed for the northern California fishery: RSH and permanent no-take reserves. Both may be useful in the management of other sea urchin populations, and some of the characteristics identified are instructive. Exploration of RSH of sea urchins was done on a YPR and EPR basis rather than including a highly uncertain stock–recruitment relationship. For various rotation periods, yield every n years was n times the yield obtained by fishing every year (Fig. 6*a*). This indicated that pulse fishing conferred no special advantage on the yield obtained from a given level of recruitment; however, such yield could probably be achieved at less cost. On the other hand, pulse fishing did have a special effect on larval production for populations with the Allee effect in fertilization described above. If there was a minimum threshold level of adult density required for successful larval production, then the population might not increase above that minimum level if fished every year but could if left alone for several years as in an RSH (Fig. 6*b*). This appears to be an inexpensive method of obtaining some robustness to the possibility of Allee effects in recruitment.

Our initial exploration of permanent reserves indicated that reserves could provide robustness to overexploitation, but at a cost in terms of yield (Quinn et al. 1993). Further investigation of this trade-off between persistence and yield revealed the similarity in the effects of effort reduction and marine reserves (e.g., Hastings and Botsford 1999). Marine reserves will increase yield in sea urchin fisheries only if ef-

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fort has substantially reduced recruitment. As can be seen in Fig. 2, whether a specific amount of effort (and reduction in LEP) has caused recruitment to decrease depends on the slope of the egg–recruitment relationship at the origin. For low values of slope, the current fishing mortality rate is likely to have reduced recruitment, while for high values, LEP can decrease substantially without reducing recruitment. Because reserves increase egg production while reducing catch by removing some areas from harvest, their net effect on catch depends on whether egg production has been reduced to the point that recruitment has declined (Botsford et al. 2004). Because the slope of the egg–recruitment relationship is critical, but not known, we assessed the potential advantage of marine reserves as a formal decision analysis based on a prior distribution of its value for this population (Botsford et al. 1999). The relative values of expected yield over the distribution of prior slopes indicated that placing about 16% of the coastline in reserves would provide the maximum long-term yield. The other significant uncertainty in the effectiveness of marine reserves, dispersal distance, was accounted for in another decision analysis (Morgan and Botsford 2001).

New Brunswick

Attempts since the early 1970s to start a green sea urchin fishery in the western Bay of Fundy have been sustained since the 1987–1988 season. Landings peaked at 1900 t in 1996–1997. Two management areas are both regulated by limited entry, specified fishing seasons, a 50-mm size limit, and a requirement to sort and cull the catch at sea. Licensees can choose to fish by either diving or dragging. In the Grand Manan Island management area, all have chosen dragging. In 1996, a TAC was set at 979 t, 3.3% of the commercial biomass in a 1992–1994 dive survey. This was reduced to 778 t in 2001 after the fleet was unable to catch the TAC. The TAC is divided into annual boat quotas with daily monitoring of the catch at the point of landing. In the mainland management area, licenses are approximately evenly divided between dragging and diving. They have had a TAC of 900 t since 1996, also based on a diving survey. This was set at a higher percentage of the commercial biomass (6.6%) because of a wider size distribution indicative of more reliable recruitment (Department of Fisheries and Oceans 2000).

Nova Scotia

In the early 1980s, an amoeboid pathogen killed 270 000 t of the green sea urchin population in Nova Scotia. By 1990, the population had recovered enough to support a small fishery and this increased to a peak of 1300 t in the 1996–1997 season. In 1995, mortalities recurred and have continued to expand through 2002 with 700 km of the outer (Atlantic) coast impacted.

The fishery is by diving only with a size limit of 50 mm and a requirement to leave the discarded urchin catch on the fishing grounds. In most of the fishery, harvesting occurs in grazing fronts within a few metres of the deep (seaward) edge of macrophyte beds. Resource assessment consists of measuring the length of these fronts, and the number of licenses allocated is based on this length (Miller and Nolan 2000). There are two types of licenses. Restricted zone licenses are each allocated an exclusive fishing area. In exchange for exclusive access, licensees are expected to fully use and enhance the habitat carrying capacity. Enhancement is accomplished by manipulating the urchin stock and its macrophyte food to maintain a productive balance. Maintaining the feeding front at 6 m or deeper was adopted as a working definition of this balance. The zones are audited by the management agency to determine if the licensees are fulfilling their commitments. The second type of license, competitive, can fish locations not assigned to zones. There has been limited entry since the fishery inception, and the zones impose another physical limit on the number of licenses.

Maine

In Maine, green sea urchins had been fished for domestic markets along the US east coast since 1929 (Andrew et al. 2002). In 1987, fishing for the Japanese market increased dramatically (Fig. 3). The market peaked in 1992–1993 and then declined to a third of the peak catch. Initial management efforts in 1992 were aimed at decreasing effort but were largely ineffective. In 1993, a size limit of 51 mm was introduced, and in 2000–2001, an upper size limit of 89 mm was tried for 1 year and then reduced to 77 mm. Six unfished reference areas of about 300 m in length have been created.

Recent analyses of catch, effort, and size data have increased the understanding of sea urchin fisheries in Maine. Vadas et al. (2002) used an estimation method similar to that of Smith et al. (1998) to identify the existence of two different growth morphs, a finding that may have implications for management. Application of a Bayesian estimation method to 5 years of size data, 14 years of catch data, and 7 years of effort data has led to estimation of natural mortality, the slope of the egg–recruit relationship (h), carrying capacity, and catchability for this fishery (Chen and Hunter 2003). In this instance, as in other recent sea urchin fisheries, when one considers the age of first maturity (4 years in this case; Vadas et al. 2002), the number of years of egg–recruit pairs is marginal for the estimation of the egg–recruit relationship.

Summary

To summarize the use of reference points by North American sea urchin fisheries, several make use of the logistic or surplus production model to set TRPs, with Alaska, British Columbia, and New Brunswick taking a specified fraction of estimated current biomass and British Columbia green sea urchins taking a specified fraction of estimated unexploited biomass. Washington, Oregon, and California do not include reference points formally in their management plans, although researchers have assessed the use of yield versus effort relationships for RSH in Washington and the use of LEP as an LRP in California. Nova Scotia utilizes monitoring of the relative abundance of the next lower trophic level. Management of the British Columbia green sea urchins refers to MSY as the LRP, but that approach involves no monitoring of the population.

Biological reference points for sea urchins

Essentially three different approaches to reference points have been taken for sea urchin fisheries: (*i*) use of logistic-based models, (*ii*) computation of LEP, and (*iii*) monitoring

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of an ecological relationship. The former two have implications for sea urchin populations (and populations of other invertebrates) around the world, while the last may be useable only for sea urchin populations in specific ecosystems.

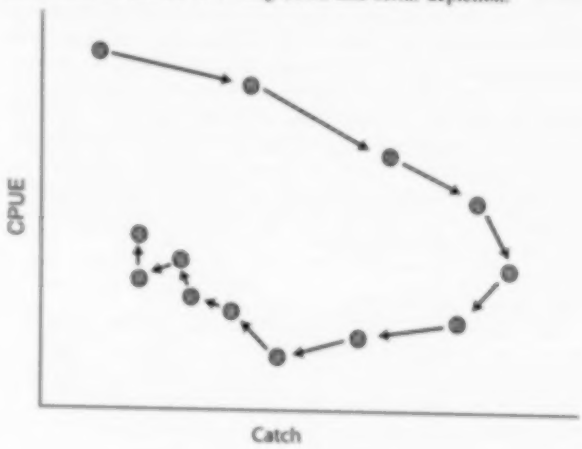
Logistic (surplus production) models

The use of logistic-based models to formulate reference points for sea urchin management is based on recommendations of methods for precautionary management when there are limited data (Garcia et al. 1989; Gabriel and Mace 1999). They make use of an approach to fishery modeling with a long history (Schaeffer 1954; Gulland 1977). Typically, the precautionary approach is to set the LRP at the fishing mortality rate that is estimated to produce the MSY and the TRP at a lower value of fishing mortality rate (e.g., as in the green sea urchin in British Columbia; Perry et al. 2001).

Potential problems with this approach stem from two sources: (*i*) mechanisms controlling dynamics may not be included in the logistic model and (*ii*) even if all relevant mechanisms were included, the data could be from a nonequilibrium state, while relationships assuming equilibrium are typically used to fit the model. This is especially problematic when the only data available are catch and effort data. Since most of the sea urchin fisheries developed rapidly, nonequilibrium conditions dominate the data, and neither of the two most important mechanisms underlying the dynamics, (*i*) fishers' movement over space in response to density (i.e., serial depletion) and (*ii*) fishing down the size structure, is included in the logistic model. The logistic model represents only the simplest caricature of density-dependent population growth (i.e., an exponential growth term multiplied by a term that declines from 1 to 0 linearly with density), and removal by fishing, and includes neither age structure nor spatial aspects.

Typical behavior of sea urchin data in terms of a logistic model can be illustrated in a plot of CPUE versus fishing effort (Fig. 7). The simplest method for fitting the logistic model is to fit a linear regression through these data, based on a relationship that follows from assuming that the logistic model is at equilibrium. That fit would be attempting to determine the linear decline in equilibrium abundance (indexed by CPUE) with effort that follows from the logistic model. However, that is not the mechanism producing these data in an actual developing sea urchin fishery. A new fishery begins with initial low effort leading to high CPUE as the initial point in Fig. 7. The subsequent decline in the plot of CPUE versus fishing effort would be determined by movement of the fishers between areas of high initial density and the fishing down of size classes at those densities. This transient period can last 5 years or more, as it did at least in the northern California fishery, the fishery in British Columbia for green sea urchins (Perry et al. 2001), and catch and effort data from the fishery in Maine (Chen and Hunter 2003). The slope would be determined by the size of the fleet, catchability, and the concentration profile of the sea urchins (Prince and Hilborn 1998) as well as the initial size structure, natural mortality rate, and growth rate. These transient mechanisms are not represented in the logistic model. After several years, catch would typically level off as the fishery became recruitment dominated, harvesting each age-class as it grew into the legal size range, and effort would begin to decline as fishers dropped out of the fishery, causing points in Fig. 7 to move upward and to the left. At that point, CPUE would either decline or increase (as shown in the Fig. 7), depending on whether fishers continued to leave. Near this time, the dynamics would finally begin to be controlled by the factors actually included in the logistic model, but unless some other factor changed abundance or effort, there would not be enough contrast in the data to fit a model.

Fig. 7. Schematic view of how a plot of annual catch-per-unit-effort (CPUE) versus effort data might vary in a sea urchin fishery with transient effects of fishing down and serial depletion.



The ultimate question in using a logistic approach to reference points is what does a fit to the logistic model tell one about population persistence or sustainable levels of fishing? What values of the parameters of a logistic model are a regression through the points shown in Fig. 7 likely to produce? Logistic-based LRPs depend on the estimate of carrying capacity in the logistic model. Whether it was biased high or low would depend on the details of the transient mechanisms, sequential depletion, and fishing down, not on the dynamics of the logistic model. It is disturbing that the levels of effort over which the regression is fit include values so high that they would likely not be sustainable, yet the fitted equilibrium model portrays them as part of the fishery dynamics. Admittedly, such a regression is based on an equilibrium assumption, but more dynamic methods of fitting would not avoid merely reflecting the effects of fishing down, serial depletion, and fishers leaving the fishery.

Lifetime egg production

LEP is commonly used as an LRP in other fisheries but was calculated for only one of the world's sea urchin fisheries, northern California, and even there, it is not an identified part of management. The reason that it is used so seldom is probably that it is usually computed from estimates of growth, fecundity, and mortality rates, thus requiring more data than are easily available in a fishery in which age is difficult to determine. This obstacle may be circumvented by the use of methods for estimating growth and mortality from size distributions and size increment data (e.g., as in Smith et al. 1998; Morgan et al. 2000).

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The advantage of LEP as an indicator is that it is directly related to population persistence, as noted in the discussion above. The fact that we do not know the limit that should be placed on this indicator might be taken as a disadvantage, but it may be better viewed as a fundamental uncertainty in managing fisheries. If we do not know how much we can reduce the factor that probably most directly determines population persistence, i.e., population growth rate, that seems to be an issue to be confronted rather than merely searching for another approach to LRPs. A more substantial drawback to LEP as an indicator is that the estimate of the fraction of natural LEP is very sensitive to the value of natural mortality rate used (Goodyear 1993).

Macrophyte monitoring

Use of the bathymetric position of the feeding front between sea urchins and macroalgae as a reference point in Nova Scotia is surely unique. It is made possible by the simplicity of the food chain and the cross-shore orientation of its components. Such conditions may not exist or may not have been detected for other sea urchin fisheries.

This reference indicator is designed to keep the fished sea urchin population below "carrying capacity" within the feeding front; hence, it is a TRP. This resembles the qualitative interpretation of logistic (surplus production) models of fishing: the highest catch is obtained where the abundance has been reduced below the carrying capacity where population growth rate goes to zero. However, the carrying capacity in this case is not necessarily a stable state; if the sea urchins are allowed to reach densities greater than ~2 kg·m^{-2}, the sea urchins would overgraze the macrophyte beds, leaving only barrens (Breen and Mann 1976). The macrophyte reference point has one characteristic of an LRP by virtue of the fact that it involves monitoring and direct feedback to fishing effort.

Implementation of reference points

The choice of reference points should depend on ease of implementation as well as their performance. With regard to LRPs, LEP directly reflects population persistence, but reference points based on the logistic model are probably easier to implement, as they require only catch and effort data. As noted above, the parameters from a fit of the logistic model to catch and effort data from a developing sea urchin fishery may well be determined by the transient effect of fishing down and the spatial effect of serial depletion instead of the decline in equilibrium CPUE with effort that is described in the logistic model. The choice then is between a model that requires information on growth, mortality, and fecundity, but reflects population persistence, and a model that requires only catch and effort data, but is unrelated to population persistence. Multiplying the results of the latter by an arbitrary constant will not improve its performance. On the other hand, having some nonzero level of biomass at which fishing will be curtailed, regardless of whether it is arbitrarily chosen, is safer than not having one at all.

Discussion

The most significant problem in the management of sea urchin fisheries does not directly involve the development of biological reference points but rather the transient effects early in fisheries development that are also mentioned in the precautionary approach. Catch rates are highest in the initial phase of sea urchin fisheries because of both fishing down and serial depletion, leading to effort levels that are not sustainable (Hilborn and Siebert 1988; Prince and Hilborn 1998). Because effort is difficult to reduce, a precautionary approach attempted after an initial period of unlimited development will be at a disadvantage. New fisheries need to limit effort and to track transient dynamic mechanisms as a new fishery develops (Miller 1999). Information from size distributions, which can even be taken from the catch, will track the fishing down effect. Information from catch reported by location, at least to the level of port, but ideally at a finer resolution, will provide information on serial depletion. Both of these provide information that can be used to set biological reference points as soon as possible. Perry et al. (1999) provided other informative examples of the problems in developing invertebrate fisheries.

Although each of the LRPs examined has inherent limitations, implementing one of them would nonetheless provide for better management if introduced with some form of population monitoring beyond just catch and effort data. Logistic-based LRPs are problematic because of the difficulty in interpreting the parameter values that will likely result from rapidly developing fisheries. Multiplying the estimated initial biomass by a fraction is a valuable conservative step because of the large amount of uncertainty involved in using this LRP. Continuing to monitor extant biomass is a safer precautionary approach than depending on the initial estimate from the logistic model, but continuing to take a specified fraction of either could lead to population collapse.

Use of LEP as an LRP has the advantage of being a direct measure of population persistence, which can be estimated through estimates of growth and mortality rates (e.g., Smith et al. 1998; Morgan et al. 2000) and possibly with other simpler means. Ultimately, an example of the shape of an unfished size distribution will be needed. The major limitation on the LEP is that we do not yet know the sustainable limit value (i.e., the 35–50% as used in finfish fisheries). However, adoption of the LEP as a reference variable will provide a greater source of empirical data from which to estimate safe values. There is also a need to be cognizant of the sensitivity of estimates of this indicator to values of the natural mortality rate used (Goodyear 1993).

Use of the position of the macrophyte front, primarily as a TRP, is intriguing, but it will require more trials before it can be considered dependable. The fact that it involves direct monitoring of ecosystem function augments robustness to uncertainty. The allocation of fishing grounds that accompanies this reference point contributes to effort limitation.

Marine reserves may be useful in reducing the pressure on 5- to 10-year-old sea urchin fisheries in which the population has been fished down to recruitment only or overfished levels. Implementation of reserves will have a direct, and likely positive, effect on LEP, but it will be difficult to estimate because of uncertainty in the spatial scale of larval dispersal. Reserves can provide for greater persistence and may provide an increase in yield, as would other means of reducing effort. The results of both depend on how much recruitment has been diminished by the existing fishery. An

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important factor affecting reserve performance is the response of fishers to reserve implementation. A recently developed model of fisher behavior in response to running costs, distance to be traveled, expected catch, and weather in the northern California sea urchin fishery has been used to explore those effects (Wilen et al. 2001).

Continued development of models and estimation methods tailored to the kinds of data available in sea urchin fisheries will improve management. Availability of size data suggests that they be size-structured models, but the required size increment data will be somewhat expensive to obtain. The performance of estimation needs to be more transparent and empirical, with more demonstration of how methods perform on trial data sets (e.g., Smith et al. 1998; Fu and Quinn 2000). Comparison of resulting estimates among species will directly improve the effectiveness of reference points, especially metaanalyses of the fraction of natural LEP that leads to collapse.

In conclusion, world sea urchin fisheries are in need of better management, primarily in the early stages of newly developing fisheries. Greater cognizance of the dynamics of that stage can lead to greater sustainability. In the long run, the LRP most likely to provide for greater sustainability is LEP.

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PERSPECTIVE / PERSPECTIVE

Biological reference points for sea scallops (*Placopecten magellanicus*): the benefits and costs of being nearly sessile[1]

Stephen J. Smith and Paul Rago

Abstract: In this paper, we concentrate on spatial aspects of growth and reproduction for sea scallops (*Placopecten magellanicus*) to advance the general theory for development of reference points for sessile animals and to illustrate the general points with several specific examples. Nonlinear mixed effects models can be used to define the spatial distribution of growth rates and their implications for the definition of growth overfishing. We develop a basin model to illustrate that the typical "boom and bust" effects, often attributed to environmental factors, are explained equally well by spatial variations in habitat quality, spatial concentration of fisheries, and dispersal of larvae among areas. Results suggest that incentives to concentrate fishing effort in lower productivity areas may be an effective tool for reducing recruitment variation and improving yields. Reductions in fishing mortality might be possible with closed areas as they can be used to reduce the concentration of effort on high scallop densities. Further, rotational area management strategies can offer the promise of balancing demands for increased yield, prevention of recruitment overfishing, maintaining spawning reserves, and reducing habitat damage and bycatch.

Résumé : Notre contribution s'intéresse aux dimensions spatiales de la croissance et de la reproduction du pétoncle géant (*Placopecten magellanicus*) afin d'améliorer la théorie générale qui sert à l'élaboration de points de référence chez les animaux sessiles et en illustrer les aspects principaux avec plusieurs exemples spécifiques. Les modèles non linéaires à effets mixtes peuvent servir à définir la répartition spatiale des taux de croissance et leurs conséquences sur la définition de la surexploitation de la croissance. Nous avons mis au point un modèle de bassin qui illustre que les effets typiques « d'expansion et d'effondrement » qui sont souvent attribués aux facteurs environnementaux peuvent s'expliquer tout aussi bien par des variations spatiales de la qualité de l'habitat, par la concentration spatiale de la pêche et par la dispersion des larves dans les différentes régions. Nos résultats indiquent que des mesures incitatives pour concentrer l'effort de pêche dans des régions de productivité plus faible peuvent être un outil efficace pour réduire la variation du recrutement et pour améliorer les rendements. L'établissement de zones fermées peut abaisser la mortalité due à la pêche, car elles peuvent servir à réduire la concentration de l'effort de pêche dans les sites de forte densité de pétoncles. De plus, des stratégies de gestion comprenant un rotation des sites de récolte peuvent laisser espérer l'établissement d'un équilibre entre la demande d'un rendement accru, la prévention de la surexploitation du recrutement, le maintien des réserves de fraye, la réduction des dommages à l'habitat et la diminution des prises accessoires.

[Traduit par la Rédaction]

Introduction

Application of the precautionary approach to fisheries management requires the definition of target and limit biological reference points (BRP) (e.g., FAO 1996; Hilborn et al. 2001). Biological reference points are observable or calculable quantities that characterize a population's state. When used to set targets or limits, they represent a tradeoff between mankind's utilization of a living resource and the resource's life history traits and productivity. Conceptually, BRPs rest on three primary tenets. First, BRPs rely on well-founded concepts of optimal harvest rates that strike a balance be-

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tween growth and mortality. These concepts are primarily circumscribed by yield-per-recruit theory. The second tenet for BRPs requires some consideration of the renewal process — the relationship between stock size and recruitment that often involves poorly understood aspects of reproductive biology and difficult-to-quantify processes governing successful fertilization and survival from zygote to harvestable individuals. The looseness of these linkages often leads to the incorrect assertion that there is no relationship between stock size and recruitment. The third tenet that shapes the establishment of biological reference points is the suite of technical, economic, and social factors defining the fishery.

Most of the work on developing reference points has been devoted to fish species and there has been little experience with invertebrate species (Caddy 2004). As fish stocks have declined in eastern North America in recent years, a number of invertebrate fisheries have contributed to a larger part of the total landings. One of these is the sea scallop (*Placopecten magellanicus*) fishery, which occurs only in the Northwest Atlantic ranging from Cape Hatteras to Labrador. Major fishing areas are located in the US Mid-Atlantic, Canadian and US sides of Georges Bank, Bay of Fundy and approaches, German Bank, Browns Bank, around Sable Island, Middle Ground, Banquereau Bank, and on St. Pierre Bank (Fig. 1). The value of landings in 2002 was in excess of CAN$125 million from Canadian fisheries and US$201 million from US fisheries.

There are no explicit definitions of biological reference points with respect to overfishing for sea scallop (*P. magellanicus*) stocks in Canada. However, many of the recent stock status reports (e.g., DFO 1997, 1998*a*, 2002*a*) state that current levels of exploitation are not sustainable. Many different indicators for nonsustainability are used. They include model-based assessments, declining catches, declining catch rates, absence of recruitment in general or in particular areas, related observations on "ageing of size structure", and declining survey indices when available.

Management for all *P. magellanicus* populations in Canada use some form of size restrictions (meat count/minimum shell height) to ensure some spawning before commercial exploitation and to increase yield per recruit (e.g., DFO 1998*a*, 2002*a*, 2002*b*). Permanent refugia for spawning and other seasonal closures have been applied or proposed in Québec, Newfoundland, and the Bay of Fundy. Catch limits are often used for stocks in a preemptive manner and few have sufficient data to develop total biomass estimates. Enterprise allocation quota schemes have been developed for the Georges Bank (DFO 2002*b*) and Browns Bank (DFO 1998*b*) fisheries. Individual transferable quotas have been implemented for the Full Bay Scallop fleet in the Bay of Fundy (DFO 2003). In other areas, where quota management is used, total allowable catches are fished on a competitive basis.

In the US, explicit limit and target reference points have been been mandated under the Sustainable Fisheries Act (Public Law 104-297). Biological reference points for scallops in US waters are based on estimates of F_{max} from a yield-per-recruit analysis and a relative biomass target computed as the product of the spawning stock biomass per recruit (SSB/R) at F_{max} and the median level of recruitment. Biological differences in growth parameters and average recruitment levels are recognized for two broadly defined stock areas: Georges Bank and the Mid-Atlantic. Assessments are conducted for these regions, but with the exception of regulations governing access to closed areas, no explicit regulations are in place to control fishing effort between regions.

Scallop management in the US is based primarily on input controls. Stock-area specific reference points are not linked to spatially distinct effort regulations. Instead, the fishery is managed by a variety of effort regulations including restrictions on days at sea, maximum crew size, ring size, and so forth. At present, entry of new vessels into the fishery is restricted, but a large reserve of unused licenses constitutes a long-term concern for future management (NEFSC 2002). Effort is regulated by the specification of allowable days at sea. These are allocated to individual permit holders in three categories: full time, part time, and occasional. Full-time scallop vessels are allocated 120 days at sea, whereas part-time and occasional vessels are allocated 48 and 10 days, respectively. Each vessel is required to have a vessel tracking device to monitor vessel location and use of days at sea within the fishery area.

Closed areas have been implemented on Georges Bank in December 1994 to protect depleted groundfish stocks and in April 1998 in the Mid-Atlantic area specifically to restrict fishing effort on recruiting scallops. Access to closed areas on Georges Bank was allowed in 1999, 2000, and January 2001. Vessels allowed access were limited by an individual trip limit and restricted by an overall quota for scallops and a bycatch quota for yellowtail flounder. An additional condition of access was the mandatory use of 10 days at sea regardless of the duration required to attain the trip limit. Areas closed to fishing in the Mid-Atlantic in April 1998 were reopened to scallopers in June 2001. Access to these areas is controlled by a trip limit and a mandatory use of a fixed number of days at sea. The controlled-access programs to closed areas can be considered as management experiments to support the development of a revised management plan based on rotational harvest areas.

Scallops are simultaneously resilient and vulnerable to exploitation. Resiliency stems from their rapid growth, high fecundity, longevity (>12 years), and a long duration pelagic larva (>30 days) produced over a protracted spawning period (late summer to early fall). These qualities ensure rapid colonization of suitable substrates and depths. Scallop vulnerability, however, arises from the recurring colonization of areas (beds), the locations of which become well known to harvesters in mature fisheries. Avoidance responses and limited advective dispersal properties of adult scallops are insignificant relative to the speed and targeting capabilities of a modern fishing fleet. Finally, the dispersive effects of harvesting may reduce the reproductive contributions of otherwise fecund but relatively immobile adult scallops.

When animal movements are minimal and targeting capabilities of the harvesters are high, management policies for BRPs must recognize aspects of the resource concentration profile (see Prince and Hilborn 1998) and the spatial–temporal patterns of harvesting. The importance of incorporating the spatial distribution of population densities, growth, recruitment, and exploitation for sea scallops when evaluating management strategies has been long recognized by Caddy (1975, 1989), Orensanz et al. (1991), and others. To date, little or no allowance has been made for spatial variation in population characteristics or fishing effort for the yield-per-recruit

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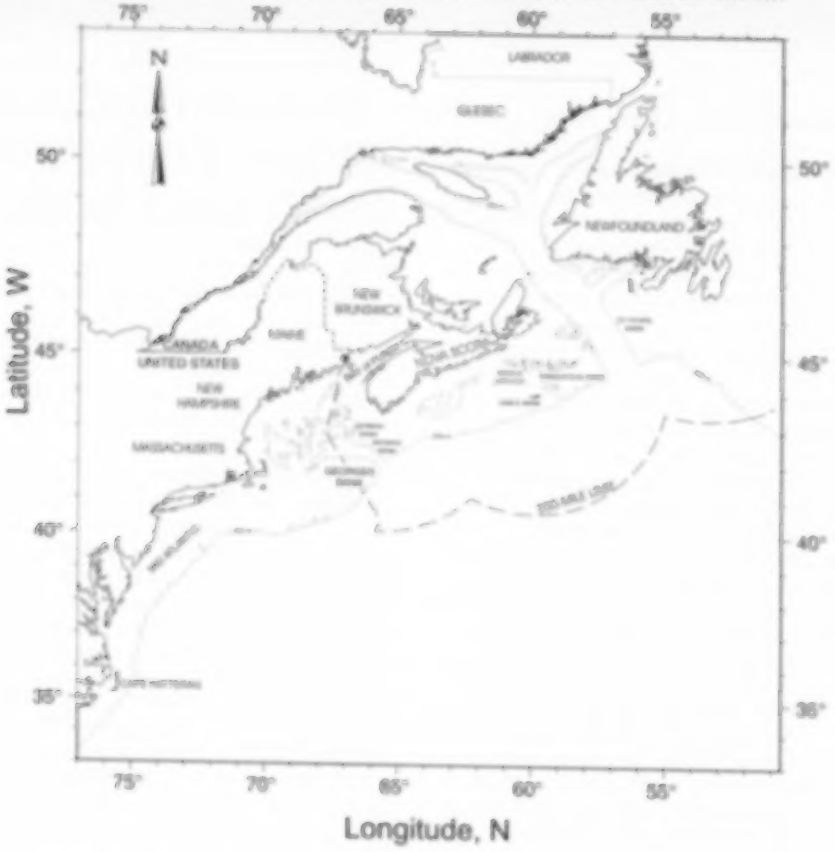
Fig. 1. Location of major fishing areas for sea scallop (*Placopecten magellanicus*) in the Northwest Atlantic.



based biological reference points that have been used for sea scallops. This may be mainly due to the lack of spatial information for most scallop stocks in the past, but recent technological innovations may soon permit the implementation of the conceptual frameworks postulated by Caddy and others nearly 30 years ago. Quantum improvements in the ability to map the resources (e.g., Stokesbury 2002; Kostylev et al. 2003), to estimate spatially distributed biological parameters (Smith et al. 2001; Lai and Kimura 2002), to link life history models with hydrodynamic models (Tremblay et al. 1994), and to census the movements of fleets through the use of satellite-based vessel monitoring systems (Robert et al. 2000; Rago and McSherry 2001) will free future reviewers of scallop BRPs from the "limbo of soft commentary" (Orensanz et al. 1998, p. 154). In anticipation of the full implementation of these innovations, we explore the implications of including spatial considerations into the definition of the traditional growth overfishing and recruitment overfishing reference points.

Growth overfishing

Growth overfishing is simply defined here as occurring when scallops are caught before they have grown large enough to maximize yield per recruit. Yield-per-recruit analysis assumes that the population is not changing with respect to character (size composition, growth rates, mortality) or size (constant recruitment) over time. Given these assumptions, the total annual yield from the population at any one time is the same as that from the fishable lifespan of any one of it's constituent year classes (Beverton and Holt 1957). Sea scallop populations have never been noted for exhibiting constant recruitment (Caddy and Gulland 1983). The impact of highly variable recruitment on defining recruitment overfishing will be discussed in the next section. In this section, we discuss how the spatial variability in growth parameters affects the definition of growth overfishing from yield-per-recruit analysis.

In general, published estimates of growth parameters for scallops are calculated for the stock as a whole, ignoring any spatial pattern (e.g., table 3 in Orensanz et al. 1991). However, growth models for scallops that incorporate spatial attributes have been presented before (see references in Smith et al. 2001). Spatial attributes are usually quite coarse, assigning individual growth curves to subareas of the population or associated with spatial proxies such as depth ranges. Although it may be recognized that growth parameters vary spatially, it is usually not clear how this information may be used when describing the population dynamics or, of interest here, defining overfishing. Here, we define a growth model

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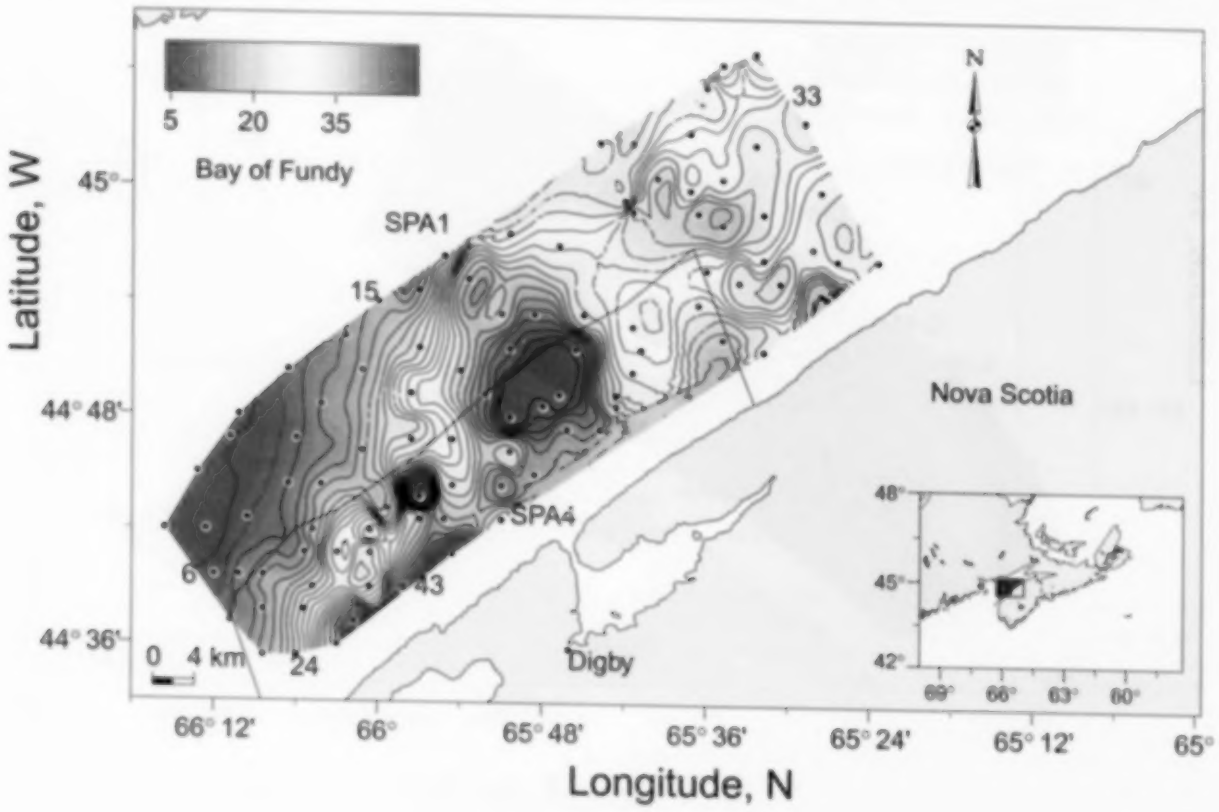
Fig. 2. Contour plot of estimates of the asymptotic weight (W_∞ (g)) from a von Bertalanffy growth mixed-effects model of meat weight as a function of age. Data from June 1996 Bay of Fundy scallop (*Placopecten magellanicus*) survey data with tow location as grouping variable. Boundary between scallop production areas (SPA) 1 and 4 is indicated on figure.



based on von Bertalanffy dynamics with individual growth characteristics associated with each spatial location. We do this by using a mixed-effects model similar to that of Smith et al. (2001) with each location as the grouping variable.

$$(1) \qquad W_{ij} = (W_\infty - w_{\infty i}) \times [1 - \exp(-(K - k_i)(a_{ij} - (T_0 - t_{0i})))] + \varepsilon_{ij}$$

where W_{ij} is the meat weight (grams) of scallop j in location i and a_{ij} is the age (years) of scallop j in location i. The fixed effects or population parameters are population asymptotic meat weight (W_∞), population Brody growth parameter (K, year^{-1}), and the population age at which $W_{ij} = 0$ (T_0). The associated random effects for location i are $w_{\infty i}$, k_i, and t_{0i}.

The random effects associated with location are all assumed to follow a Normal distribution with zero mean and variance–covariance matrix $\sigma^2\mathbf{D}_i$. For the von Bertalanffy model the variance–covariance matrix is of dimension 3×3 with diagonal elements $\sigma^2_{w_\infty}$, σ^2_k, and $\sigma^2_{t_0}$. The general procedure of fitting the nonlinear mixed effects model assumes that the variance–covariance matrix is a general positive definite matrix allowing the fitting algorithm to estimate covariances between the random effects.

For the measurements made for scallops at each location, the error associated with meat weight at each age (ε_{ij}) is also assumed to have a normal distribution with zero mean and variance–covariance matrix $\sigma^2\Lambda_i$. The matrix Λ_i is initially set to the identity matrix when fitting the model, and hence repeated measurements at the same location are assumed to be independent over age once the random effects have been accounted for.

Growth data was collected from every tow in the annual survey of scallops off Digby, Nova Scotia (scallop production areas (SPA) 1 and 4) from 1996 to 1999. To date, ages have only been determined for all of the shells in the 1996 data set. The mixed-effects model in eq. 1 was fit to these data using tow location as the grouping variable. A contour map of the random effects estimates for the W_∞ parameters (Fig. 2) shows spatial patterns consistent with bathymetric contours. Based on Beverton and Holt's (1957) suggestion that food availability would only affect the process of anabolism, we would expect that these patterns in W_∞ would reflect varying availability of food with depth (see Shumway et al. 1987).

The spatial pattern in Fig. 2 can be reexpressed in terms of F_{max} using eq. 6.21 of Quinn and Deriso (1999)

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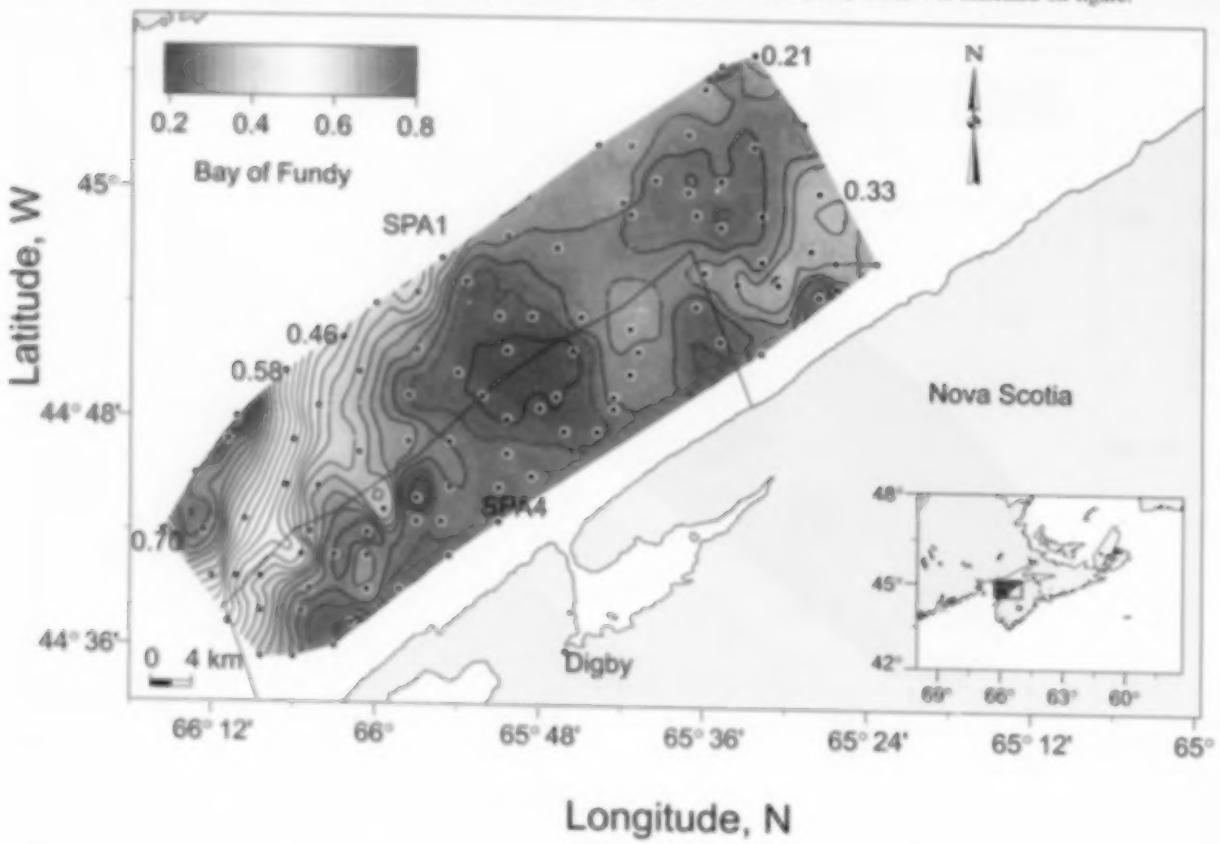
Fig. 3. Contour plot of estimates of the fishing mortality that maximizes yield-per-recruit (F_{max}) based on a von Bertalanffy growth mixed-effects model of weight as a function of age. Data from June 1996 Bay of Fundy scallop (*Placopecten magellanicus*) survey data with tow location as grouping variable. Boundary between scallop production areas (SPA) 1 and 4 is indicated on figure.



$$F_{max,i} = \frac{k_i}{\sqrt{(1 - w_{r,i}/w_{\infty,i})(1 + k_i/M)} - 1} - M \quad (2)$$

where k_i and $w_{\infty,i}$ are as defined above, M represents instantaneous annual natural mortality, and $w_{r,i}$ is the weight of a scallop when it recruits to the fishery in location i. Using this relationship and assuming a constant instantaneous annual natural mortality rate of 0.1, a spatial map of growth overfishing reference points can be derived from the mixed effects growth model results (Fig. 3). The general practice for the Bay of Fundy and many other areas is to calculate growth-overfishing reference points such as F_{max} combining all data for each area. For the 1996 data, this results in $F_{max} = 0.29$ for the Digby portion of SPA 1 and 0.31 for SPA 4. Both of the nonspatial estimates of F_{max} for each area exceed the estimate obtained for the higher growth areas in the spatial map of F_{max} (0.25) where fishing is characteristically concentrated (Fig. 3).

The mean F_{max} over all tow locations was 0.27, which is less than the equivalent estimates for either scallop production area when spatial considerations were disregarded. In 1996, densities in the high growth areas were low and the data from the survey used to calculate the nonspatial estimates for growth were dominated by scallops from the more marginal growth areas. This implies that estimates of F_{max} that ignore spatial variation in growth parameters are very vulnerable to differential settlement patterns and changing densities due to spatial exploitation patterns when calculated from survey data. Spatial estimates calculated via eq. 1 should be more robust to these effects if the survey stations are a random sample of the area.

Based on the spatial patterns then, growth overfishing would be avoided by fishing the higher growth areas at a lower rate than the lower growth areas. In practice, this would be counter to standard fishing practice and would be difficult to enforce.

Recruitment

To a greater or lesser degree, scallop fisheries oscillate between periods of low abundance and then sudden increases due to episodic recruitment (Caddy and Gulland 1983; Caddy 1989). Orensanz et al. (1991) has reviewed the evidence for relationships between stock and recruitment for most commercial species of scallops. Although some authors have identified recruitment overfishing as having occurred for

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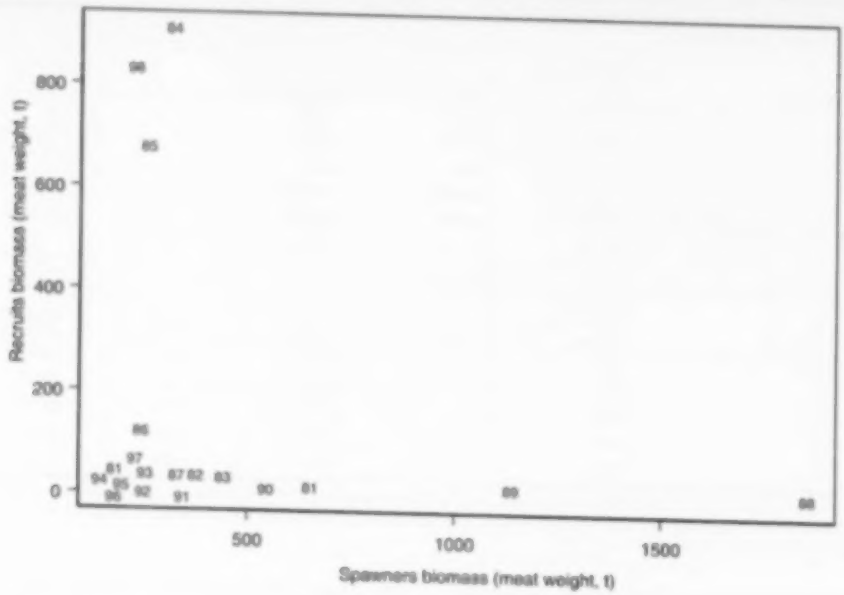
Fig. 4. Stock–recruitment data from scallop (*Placopecten magellanicus*) surveys in scallop production area 4 in the Bay of Fundy. Points are labelled by two-digit year class.



particular scallop species (e.g., Dredge 1988), others have found little evidence to identify a parametric function relating spawning stock to subsequent recruitment (e.g., Naidu 1991; Marelli et al. 1999). On the other hand, there does seem to be a positive relationship between broodstock and spat fall for scallop species in culture situations (Ito and Byakuno 1988, fig. 10).

For wild stocks of scallop species, most authors report that environmental influences on the survival of larvae may mask any such relationship if it exists at all (e.g., Caddy 1979; Hancock 1973; Joll and Caputi 1995). One exception to these conclusions is the study by McGarvey et al. (1993) who reported significant positive correlations between stock (measured as egg production) and recruitment for sea scallop on Georges Bank.

The pattern for stock and recruitment from the annual surveys in the Bay of Fundy is characteristic of that of other bivalves (e.g., cockles in Hancock 1973). In general, recruitment spikes seem to come from the smaller spawning stock sizes (Fig. 4). This interpretation does have to be tempered with the fact that the spawning stock in 1989 was decimated by a mass mortality event before the late summer spawning period (Smith and Lundy 2002). However, the subsequent recruitment from the larger 1988 spawning stock was also quite poor. Assuming environmental effects are dominant in determining year-class strength, the pattern in Fig. 4 could be interpreted to indicate that no matter what the spawning population size, there are always more than enough eggs in the water and that the few large recruitment events observed over the period of 22 years simply reflect the degree and the relatively rare occurrence of favourable environmental effects. Figure 5 of McGarvey et al. (1993) could be interpreted in the same way with the two large recruitment events coincident with the two largest spawning stock sizes simply indicating favourable environmental conditions rather than evidence for a direct stock–recruitment relationship. In either case, favourable environmental conditions are rare and the series are not long enough to have seen good recruitment over a larger range of spawning stock sizes.

As we showed earlier, there is a spatial pattern for growth parameters in the Bay of Fundy. Egg production for sea scallops has been shown to have an exponential relationship with size (Langton et al. 1987; McGarvey et al. 1992) and, therefore, will also have a similar spatial pattern. Sinclair et al. (1985) proposed that because sea scallop beds in the Northwest Atlantic and Georges Bank have been persistent for long periods of time, they must also be self-sustaining. That is, although some larvae are advected away from the spawning areas, there must be considerable local retention for the scallop beds to persist. Studies of larval transport and abundance in the Bay of Fundy found that although there was some evidence for larval transport, densities of larvae were found to be highest in areas where the greatest biomass of spawners occurred (Tremblay and Sinclair 1988). Given that the number of eggs spawned is a function of the size of the scallops and their abundance, then relationships between spawners and recruits may only be locally evident. McGarvey et al. (1993) reported that the strength of the correlations increased when relationships within and between neighbouring subareas of the northern edge and northeast peak of Georges Bank were considered.

Although higher densities of spawners should translate into higher numbers of eggs being spawned, studies of other bivalves have suggested that settlement success of the larvae and hence subsequent recruitment to the commercial fishery may exhibit a negative relationship with the local density of animals (e.g., Hancock 1973). In the case of cockles, Hancock (1973) suggested that the survival of settled larvae is

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Table 1. Settings for basin – delay difference model for a scallop (*Placopecten magellanicus*) population. See text for descriptions of the basin and delay difference models.

(*a*) Model parameters.

	Habitat type		
Parameter	Poor	Fair	Good
ρ	0.72	0.81	0.86
α	2.85	4.79	5.99
ln(*a*)	–5.5	–5.0	–4.5
b	0.001	0.0005	0.0004
Survival (natural)	0.905	0.905	0.905
Survival (fishing)	0.905	0.740	0.607

(*b*) Proportion of larval dispersal to each subarea.[a]

	Subareas				
Subareas	1 Poor	2 Fair	3 Good	4 Fair	5 Poor
1 Poor	0.75	0.12	0.06	0.05	0.02
2 Fair	0.08	0.75	0.12	0.03	0.02
3 Good	0.00	0.05	0.90	0.03	0.02
4 Fair	0.00	0.00	0.05	0.80	0.15
5 Poor	0.00	0.00	0.00	0.05	0.80

[a]For example, 0.75 of the larvae are retained in the first poor subarea, 0.12 disperse to the neighbouring fair subarea, 0.06 disperse to the centre good subarea, etc. In the second poor subarea (subarea 5), 0.15 of the larvae are lost from the system.

less likely in patches of high densities of already settled animals. The mechanisms that have been identified as being responsible for this reduced survival include competition for space among burrowing bivalves, cannibalism of larvae by settled animals, and competition for food between older animals and newly settled animals. In this context, the pattern illustrated in Fig. 4 may reflect the lower survival of larvae as population size increases.

In terms of spatial and temporal variation, we have a number of elements that may have important effects on recruitment that in turn may determine how thresholds for recruitment overfishing could be defined. They include persistent spatial patterns of growth and egg production, a degree of larval retention, density-dependent habitat suitability for larval settlement success rate as a function of spawner density (discussed below), and environmental effects on such processes as growth, larval survival, and settlement success.

We used the basin model of MacCall (1990) to explore how these elements could affect the dynamics of a population with characteristics similar to scallops in the Bay of Fundy. The population dynamics were modelled using the following form of the delay-difference model (Hilborn and Walters 1992, p. 335), which is currently used to model the scallop populations in the Digby area for the stock assessment (Smith and Lundy 2002).

$$(3) \qquad B_{t+1} = S_M S_f(\rho + \alpha/w_t)B_t + R_{t+1}$$

where B_{t+1} is the biomass of commercial-sized scallops and R_{t+1} is the biomass of recruits in year $t + 1$. Survival from natural and fishing mortality are S_M ($S_M = \exp(-M)$) and S_f ($S_f = \exp(-F)$), respectively. The growth parameters ρ and α are defined below. The average weight of commercial-sized scallops in year t is defined as w_t.

The area inhabited by the model population was set up as a simple scheme of five equal-sized subareas with the middle subarea characterized as having good habitat for scallop. The two subareas on either side of the middle subarea were classed as fair habitat and the two end subareas were classed as poor habitat.

Parameter values for the growth- and density-dependent habitat survival parameters are given in Table 1*a*. Growth was modelled using the following linear relationship between weight at age $a - 1$ (w_{a-1}) and weight at age a (Hilborn and Walters 1992):

$$(4) \qquad w_a = \alpha + \rho w_{a-1}$$

Density-dependent habitat suitability was modelled as a decreasing rate of larval settlement success as a function of increasing spawning population size assuming a Ricker stock–recruitment curve,

$$(5) \qquad R = aS\exp(-bS)$$

where R is recruitment and S is spawning stock. Spawner success or larval settlement success in the context of our model is given as

$$(6) \qquad \ln(R/S) = \ln(a) - bS$$

MacCall (1990) suggested that the term ln(a) include environmental effects on spawner fecundity and density-independent effects on offspring mortality. Density-dependent sources of mortality and reduced fecundity are included in the bS term. We use the relationship in eq. 6 to model density-dependent habitat selectivity by reducing settlement success (R/S) as a function of spawning stock. The coefficients a and b used in each of the habitat types are given in Table 1*a*.

Annual per-scallop egg production was estimated using the shell height – egg number relationship presented in Langton et al. (1987). Although Langton et al. do not give the parameters for the curves in their Fig. 2, we estimated the function to be number of eggs = shell height$^{3.7}$ based on

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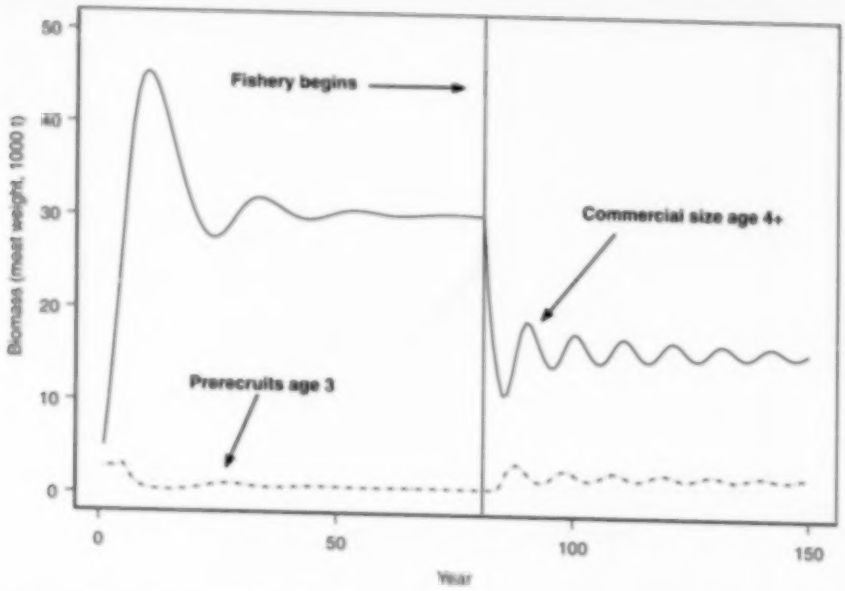
Fig. 5. Basin model results for a scallop (*Placopecten magellanicus*) population with no stochastic components. Parameter values are given in Table 1.



information given in the text. We converted this function to be in terms of meat weight instead of shell height by using the allometric relation from table 13 of Smith and Lundy (2002) for 1996 data of meat weight = exp(–11.02)shell height$^{2.94}$. That is,

$$\text{number of eggs} = \left(\frac{\text{meat weight}}{\exp(-11.02)}\right)^{3.7/2.94} \quad (7)$$

An arbitrary mean egg to larvae survival of 1 in 50 000 was assumed for investigations here.

Finally, larvae spawned in a habitat are mainly retained in that habitat, although some dispersion was allowed for. The proportion of larvae retained in each subarea or dispersing to neighboring subareas are given in Table 1*b*.

The model was run assuming that natural mortality was equal in all areas and that intensity of fishing would vary directly with the habitat suitability (Table 1*a*). For this application of the model, the total time series was set at 150 years with no fishing until year 81 to allow the population to come to equilibrium. Before the start of the fishery, the population exhibits a high stable biomass with very low recruitment (Fig. 5). Once the fishery starts, the population oscillates to a lower equilibrium with generally higher and more variable recruitment. When the population has been fished down from the unfished equilibrium, the stock–recruitment relationship roughly resembles the Digby example (Fig. 4) with the largest recruiting year classes coming from the smaller spawner biomass levels (Fig. 6).

A simple stochastic version of the model was built by setting the mean egg to larvae survival as a beta random variable with shape parameters of 1 and 49 999 to get the same mean value used above of 1 in 50 000. In this case, the biomass does not reach a stable equilibrium in the 80 years before the fishery but does stay above 21 000 t once the population has grown past the initial conditions (after year 12, Fig. 7). Recruitment is variable before the start of the fishery but this variability increases along with the level of recruitment after the fishery begins. The stock–recruitment pattern looks even more like the Digby pattern (Fig. 8) once the initial biomass has been fished down (after year 5).

For both forms of the model, the time series of catch exhibits periodicities similar to those reported for the Bay of Fundy fishery (Fig. 9). Periodicities in the Bay of Fundy catch series have been previously reported as indicative of periodic environmental effects on recruitment (Dickie 1955; Caddy 1979).

Recruitment overfishing

Recruitment overfishing is generally assumed to occur when the spawning stock biomass has been reduced by fishing to a point at which reproduction is impaired in some sense. In the standard stock–recruitment presentation such as that given in Fig. 4, the implicit assumption is made that the reproductive productivity for individuals at high and low stock sizes is the same. In the Bay of Fundy, the larger stock sizes were due to large recruiting year classes and, hence, mainly consisted of small scallops. As scallops show an almost linear increase in gamete production with meat weight (ref. eq. 7), the productivity of the larger stock sizes such as in 1988 and 1989 (Fig. 4) will be a function not only of stock size, but also of the average meat weight of the scallops in the population. In fact, the average meat weights for these two years were 9.4 g and 11.1 g, respectively. In 1984 and 1985, the average meat weights were 17.5 g and 17.7 g, respectively, and on a per-scallop basis, the scallops from these smaller year classes should have produced between 1.8 and 2.2 times the number eggs produced by individuals from the larger year classes.

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Fig. 6. Stock–recruitment scatter plot during fishery period in the nonstochastic version of basin model.

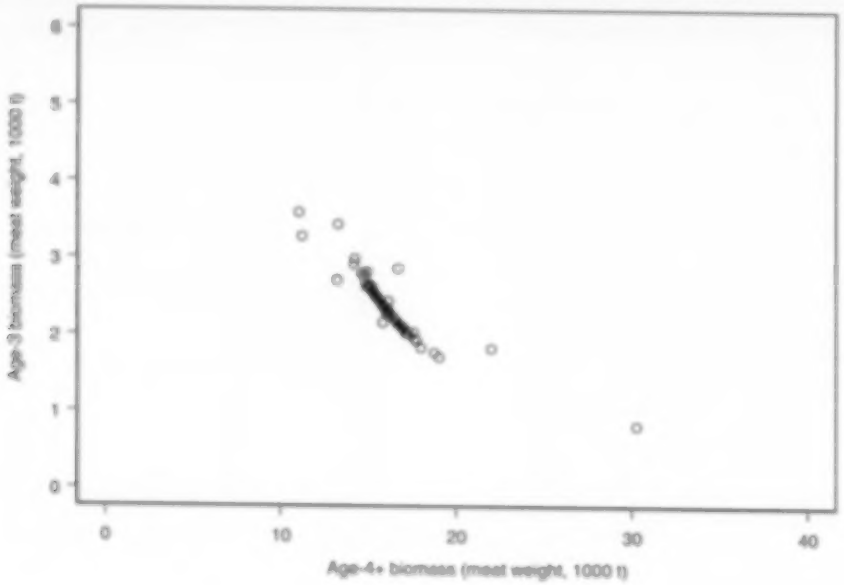
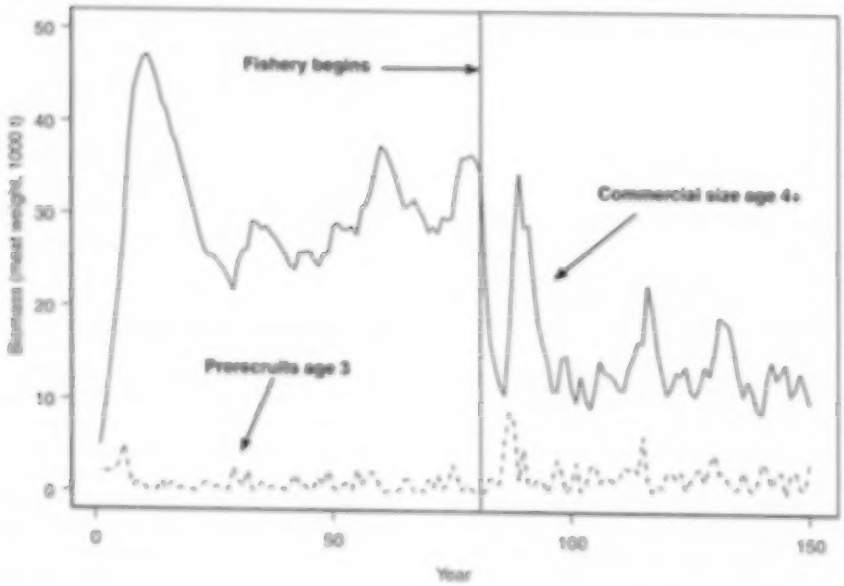


Fig. 7. Basin model results for a scallop (*Placopecten magellanicus*) population with stochastic component for fertilization and egg to larval survival. Parameter values are given in Table 1.



In the basin model for the unexploited period (years 1 to 80), the larger stock sizes were characterized by the larger meat weights. However, for the exploited phase of years 81 to 150, the average meat weights were smaller for the larger stock sizes. Thus, the model suggests that smaller average sizes reflect unrealized biomass per recruit when fishing mortality is high. Hart (2003) demonstrated a similar phenomenon for Georges Bank scallops protected from fishing mortality in closed areas.

The traditional definitions of an equilibrium recruitment level that replaces spawning stock implicit in replacement reference points (e.g., F_{msy}, F_{rep}; Quinn and Deriso 1999) is complicated here by the size composition of the larger spawning stock sizes. For scallops, we can start with assuming that at least one egg per spawner has to survive to one female recruit as a basis for replacement. At equilibrium, the discounted sum of eggs released by a female recruit must produce two recruits (assuming 1:1 sex ratio) that survive

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Fig. 8. Stock–recruitment scatter plot during fishery period in stochastic version of basin model.

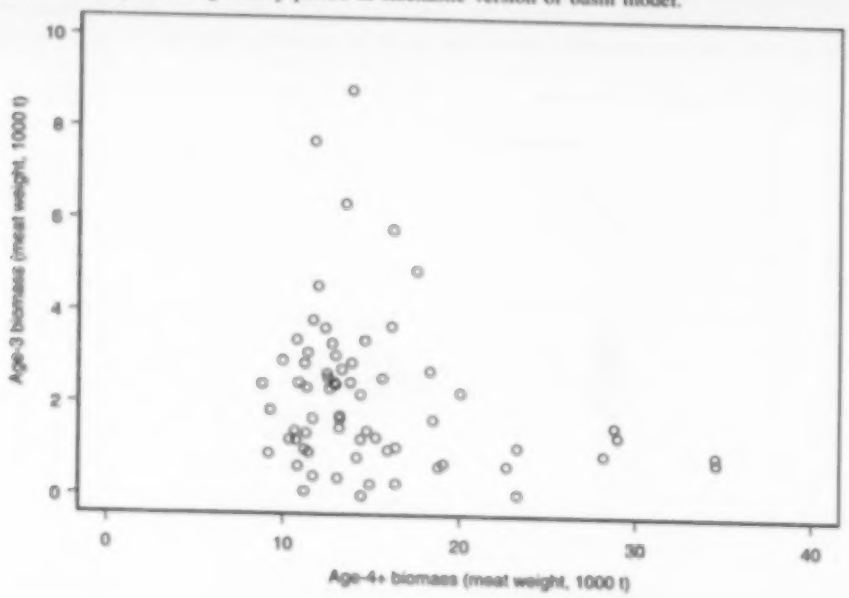
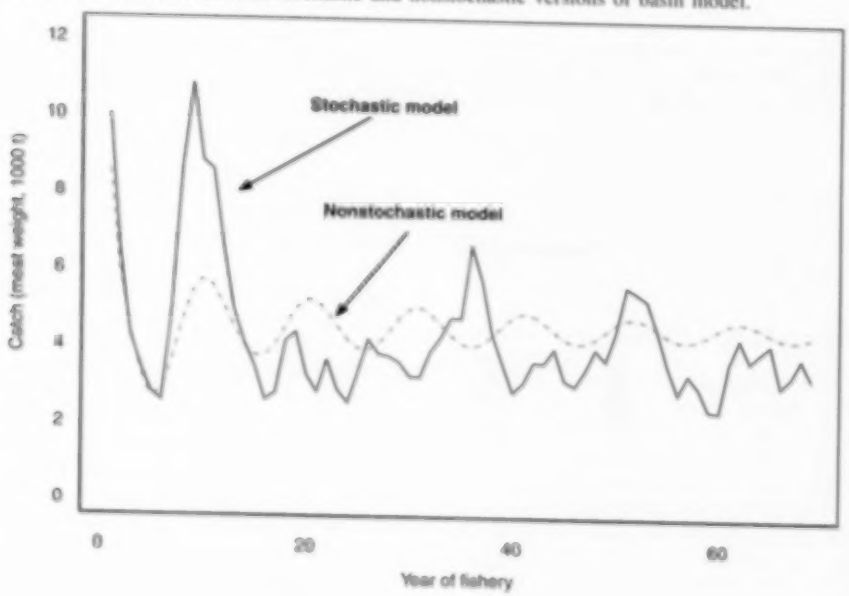


Fig. 9. Comparison of time series of catches from stochastic and nonstochastic versions of basin model.



the larval stages, settlement, and life on the bottom through to ages 1 to 4 years (e.g., Vaughan and Saila 1976). For the moment, we will assume that fertilization success for all eggs released was constant and density-independent. The baseline survival for replacement is simply 2 divided by the number of eggs produced. Because the number of eggs produced increases with the size of the animal, this replacement can occur at progressively lower rates of survival for larger animals (Fig. 10). For fishing years in the basin model, survival (the number of recruits at age 4 divided by the number of eggs from which the cohort originated) is rarely above the replacement line except for the larger scallops in the good habitat area. Egg production in the poor habitat areas is not enough for the population to persist because of the relatively small size of the scallops and associated gonads in these areas. It is only the addition of larvae from the adjacent areas that keeps the population in the poor areas from going extinct. The population in the poor areas goes extinct before

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Fig. 10. Survival rates from egg to 4 years old for nonfishery period of stochastic version of basin model. Number of eggs calculated from meat weight – egg number relationship in eq. 7. Replacement line refers to a survival such that a minimum of two recruits (assuming 1:1 sex ratio) survive the larval stages, settlement, and life on the bottom through ages 1 to 4 years. Good habitat, ○; fair habitat, +; poor habitat, △.

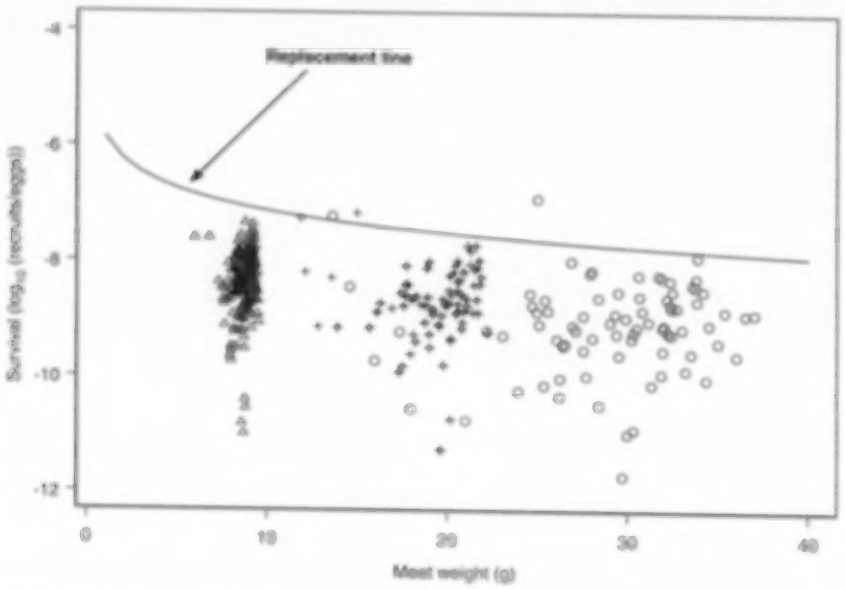
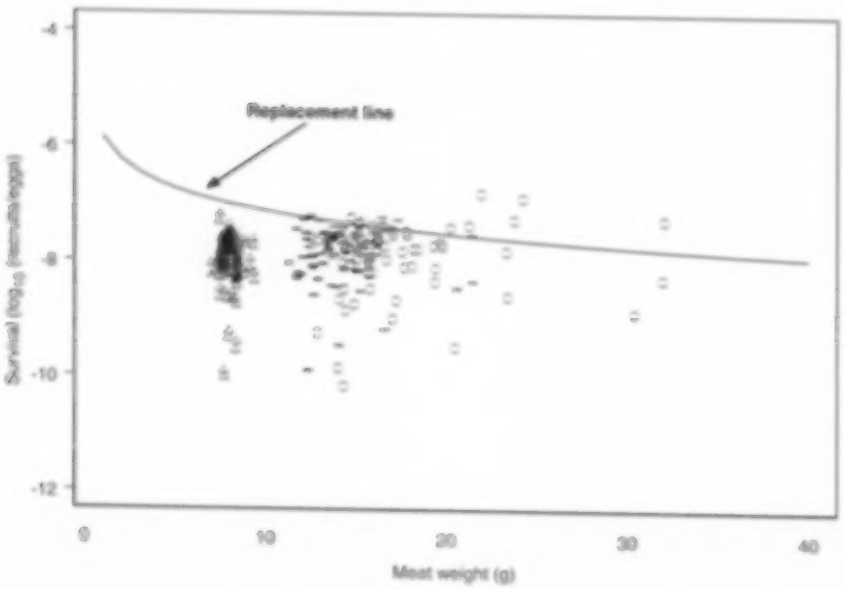


Fig. 11. Survival rates from egg to 4 years old for fishery period of stochastic version of basin model. Number of eggs calculated from meat weight – egg number relationship in eq. 7. Replacement line refers to a survival such that a minimum of two recruits (assuming 1:1 sex ratio) survive the larval stages, settlement, and life on the bottom through ages 1 to 4 years. Good habitat, ○; fair habitat, +; poor habitat, △.



the fishery starts when the dispersion matrix in Table 1*b* is replaced with the identity matrix (no dispersion). In the years before the fishery began, survival was rarely above the replacement line in all habitat types, mainly because carrying capacity had been reached quickly and density-dependent habitat selectivity became a factor in reducing settlement survival (Fig. 11). Therefore, the evaluation of whether or not egg production is enough to replace the

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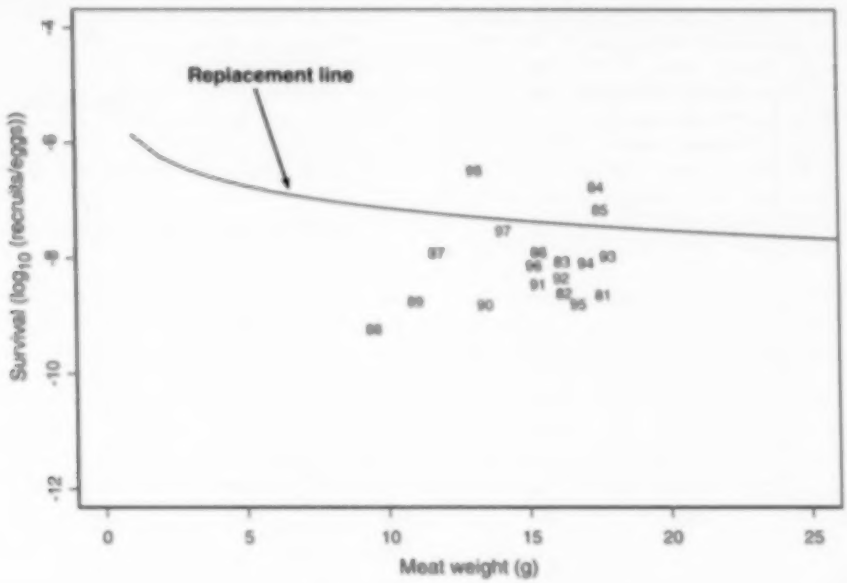
Fig. 12. Estimated survival rates from egg to 4 years old for scallops (*Placopecten magellanicus*) in scallop production area 4 based on delay-difference model in Smith and Lundy (2002). Replacement line refers to a survival such that a minimum of two recruits (assuming 1:1 sex ratio) survive the larval stages, settlement, and life on the bottom through ages 1 to 4 years. Points labelled by two-digit year class.



spawning stock depends very much on whether the stock is highly exploited or not. For the parameters used in the basin model, it appears that it is mainly the egg production in the good habitat area that is driving the population increases during the exploited phase (as seen in Fig. 7).

We evaluated the survival for scallop production area 4 in the Bay of Fundy by ignoring spatial effects and estimating survival rates over the whole area for each cohort to 4 years of age from 1981 to 1998. Again, assuming that the egg – meat weight relationship holds here, we see that there have only been 3 out of 18 years in which survival was such that the number of recruits exceeded the number needed for replacement (Fig. 12). Although these increases were probably due to recruitment from the good habitat areas identified by growth characteristics in Fig. 2, we will continue with this example at the aggregate level. Assuming that densities are not high enough to invoke serious density-dependent habitat selectivity effects, this figure suggests a metric that may be useful as a reference point. That is, based on the observed data, determine the probability that survival will exceed the replacement line survival limit if the average meat weight in the population is X g. For example, at an average meat weight of 12 g, 3 of the 18 survival rates exceeded the replacement line value. However, if the meat weight in 1997 had been larger, say 17 g, then the survival rate for that year would have been high enough to exceed the replacement line. If we assume that survival rate is independent of meat weight, then we can use these modelled survival rates as representative of those that we may encounter in the future and calculate for each meat weight what proportion of the observed rates were above or below the replacement line. These calculations indicate that for an average meat weight of 17 g, there is only a 22% probability of recruitment equaling or exceeding the replacement line for spawning stock — assuming 100% constant density-independent fertilization success. Lower rates of fertilization success will reduce this probability.

One of the open questions in this investigation concerns fertilization success and how it is affected by the density of the spawning scallops. In the next section, we turn to this question using a different set of models.

Density-dependent fertilization rate

Langton et al. (1987) suggest that year-class success of scallops may be more closely related to degree of spawning synchrony than to total reproductive output. For sessile sexual species with limited dispersal of gametes, it is obvious that a large biomass is irrelevant if interanimal distances are too great for successful fertilization. Some of the earliest research on bay scallops (*Argopecten irradians*) suggested the possibility of sperm limitation in natural populations (Belding 1910). Stotz and Gonzalez (1997) suggested that exploitation of *Argopecten purpuratus* populations had resulted in the complete elimination of scallop beds. Orensanz et al. (1991) recognized that prevention of recruitment overfishing required careful consideration of the biology of the species. They noted that if the threshold density for fertilization success exceeded the threshold for economic profitability, then more drastic measures to preserve spawning areas would be necessary.

Empirical data on fertilization success in natural populations are rare and generally qualitative (Levitan and Sewell 1998). Stokesbury (1999) examined spatial distributions at a

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Fig. 13. Comparison of model-based relative increase in fertilized scallop eggs for Georges Bank and Mid-Atlantic areas surveyed by NMFS R/V *Albatross* 1980–2000. Results are expressed as a ratio of annual value to the 1980 to 1995 mean. Closed areas on Georges Bank began in December 1994; closed areas in the Mid-Atlantic region were put in place in April 1998.

scale of centimetres and found aggregations or "clumps" that might be important for ensuring high levels of fertilization. He further suggested, but did not verify experimentally, that scallop movements may be directional to support the formation of clumps. If so, disruption by fishing activity could reduce fertilization rates and subsequent spawning success. Fine-scale aggregations may also facilitate the neurosecretory regulation of spawning. Barber and Blake (1991) summarized a number of studies on a variety of species (*Chlamys varia*, *Patinopecten yessoensis*, *Pecten albicans*) in which release of neurosecretory products was necessary before external stimuli can induce spawning. Hence the "clumps" may be important for synchronization of spawning activities. Quinn et al.'s (1993) modelling of sea urchin populations suggested that the protection of high-density refuges would be a way of protecting against high rates of exploitation.

Claereboudt (1999) developed a fine-scale three-dimensional simulation model of the fertilization process and parameterized it for *P. magellanicus*. His model allowed for variation in initial density, an aggregation coefficient similar to the "concentration factor" of Prince and Hilborn (1998), and variation in exploitation. Egg production scaled linearly with density, but larvae density declined by over 95% when a simulated stochastic population was subjected to harvest rates on the order of 50%. The nonlinear response to exploitation arose due to increased distances between randomly distributed individuals.

Although field data that confirm or refute the concept of localized recruitment overfishing are not available for *P. magellanicus* stocks, we can use the results of Claereboudt's model to investigate the relative increase in fertilized egg production since closed areas were used as management tools in the USA fishery. As suggested in Claerboudt's figure 3, fertilization success increases linearly with density (number·m^{-2}). If we approximate the fertilization coefficient in Claereboudt's figure 3 as 0.2, then the number of fertilized eggs is proportional to the product of the fertilization rate and stock biomass. We used the following piecewise linear model to develop an index of fertilized egg production:

$$(8) \qquad E_{\text{Fert}} = \min(0.2D,1)B$$

where D is relative density ((number·tow^{-1})·(m^2·tow^{-1})$^{-1}$, dredge efficiency $^{-1}$) and B is the estimated total weight of scallop meats per tow. In this exploratory computation, we use a gear efficiency rate of 40% and conservatively assume that egg production is proportional to somatic weight. Average egg production per tow is estimated as the simple average of the n tows sampled each year in the Georges Bank and Mid-Atlantic regions. A time series of such estimates (Fig. 13) illustrates the remarkable increase in the model-based fertilized egg output since the closed areas were instituted. These results suggest that the egg output from the regions has increased by several orders of magnitude since 1994 on Georges Bank and since 1998 in the Mid-Atlantic region.

The methodology that we used does not account for the potential reproduction of localized clusters that might be masked by the overall density estimate based on catch rate data from the fishery or surveys. In unfished scallop beds in Baie des Chaleurs, Quebec, Stokesbury and Himmelman (1993) found most scallops within small clusters of <4.5 individuals·m^{-2}, with nearest-neighbor distances of <100 cm. For the US dredge survey, an average density half as great in one tow versus another could mean either half as many clusters per unit area or the same number of clusters with half as many scallops per cluster. In the former case, effective egg produc-

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tion would scale with biomass. In the latter case, the average distance would double and eq. 8 would apply. Neither extreme is likely to apply because dredges are not 100% efficient. Thus lower average densities are likely to result from some combination of reduced numbers of clusters and densities within clusters. The projected increases in egg production in Fig. 13 therefore could be viewed as upper bounds if nearest-neighbor distances scaled directly with average density. Despite the coarse scale of these comparisons, the model results suggest that the prospects for refining our understanding of stock–recruitment relationships are greatly enhanced.

Recruitment overfishing and closed areas

We note that the recruits to an area A (R_A) are a function of the total number of fertilized eggs produced (E_{TOT}), the survival from the pelagic stage through settlement (S_0), and the initial suitability of the habitat (ξ_A). The number of fertilized eggs produced at location A (Egg_A) is a function of the total fecundity of females, say $h(W_A)$, and the average distance between males and females. Of particular importance to scallops dynamics is the observation that egg production increases by about the 4th power of shell height (McGarvey et al. 1992). Thus potential egg production increases even faster than biomass when fishing mortality is reduced. Claereboudt's (1999) physical simulation model gives some insights into advective and diffusion factors that govern fertilization success. Let $g(D_A)$ represent the function of density that defines the distribution of average interscallop distance. Then we can write

$$\text{Egg}_{\text{TOT}}(t) = \sum_A g(D_A(t))\, h(W_A(t)) \tag{9}$$

The potential pool of recruits is product of a density-independent survival rate S_0 and the total egg production,

$$R_T(t) = S_0 \text{Egg}_{\text{TOT}}(t) \tag{10}$$

and the actual rerecruitment in area A is defined as

$$R_A(t) = \xi_A R_T(t) \tag{11}$$

Assuming that the initial survival rate S_0 is independent of stock size, the variance of recruitment at location A can be approximated by the delta method as

$$\begin{aligned} V(R_A(t)) &= V\left(\xi_A S_0 \sum_A g(D_A(t))\, h(B_A(t))\right) \\ &= \xi_A^2 V\left(S_0 \sum_A g(D_A(t)) h(B_A(t))\right) \\ &= \xi_A^2 \left\{ E\left[\sum_A g(D_A(t))\, h(B_A(t))\right]^2 V[S_0] \right. \\ &\quad + E[S_0]^2 V\left[\sum_A g(D_A(t))\, h(B_A(t))\right] \\ &\quad \left. + V[S_0] V\left[\sum_A g(D_A(t))\, h(B_A(t))\right]\right\} \end{aligned} \tag{12}$$

Equation 12 can be simplified as $g(\cdot)$ and $h(\cdot)$ are both decreasing functions of fishing mortality because average distances between individuals increase and total biomass decreases with increasing fishing mortality (or effort). As the variance of density decreases with density, the variance of recruitment at location A will decrease with increasing fishing mortality. In the above equation, the variance of $R_A(t)$ will become dominated by the variance of the survival rate S_0. On the basis of this model, high levels of fishing mortality will induce greater apparent variability in recruitment, thereby reducing the ability to identify a functional relationship between spawning stock and recruitment. More precisely, high levels of fishing mortality will reduce the ability to understand the underlying mechanisms governing recruitment success.

Can reserves improve recruitment? Suppose that an area is arbitrarily divided into a region open to fishing and a permanent marine reserve. Let D_A^* and B_A^* denote average density and biomass per unit area in the reserve or closed area. In general, these values would be expected to exceed the densities associated with maximum sustainable yield. The expected total recruitment is defined as follows:

$$R_T^* = S_0\left(\sum_{A\in\text{Open}} g(D_A(t))\, h(B_A(t)) + \sum_{A\in\text{Reserve}} g\,(D_A^*(t))\, h(B_A^*(t))\right) \tag{13}$$

and the corresponding variance is defined as

$$V(R_A(t)) = V\left[\xi_A S_0\left(\sum_{A\in\text{Open}} g(D_A(t))\, h(B_A(t)) + \sum_{A\in\text{Reserve}} g\,(D_A^*(t))\, h(B_A^*(t))\right)\right] \tag{14}$$

Equations 13 and 14 provide a generalized prediction of the expected recruitment from a spatially distributed population consisting of subareas open and closed to fishing. Total recruitment and its variance will increase when an area is closed to fishing if the effort in the previously open area does not redistribute to the remaining open areas, thereby increasing fishing mortality in these areas. When redistribution of effort occurs, the consequences for total recruitment will depend on initial spatial distribution of effort, the growth rate of individuals, and the proportion of the area closed. It is clear, however, that total recruitment will be derived from components with low and high expected egg production and concomitant variance levels. Closure areas would be sufficient to increase total recruitment if the increase in egg production in the closed areas exceeds the fishing mortality induced loss of egg production in the open areas.

The reserve generates potential benefits of increased recruits and immediate costs of lost yield. The relevant issue is whether the short-term yield losses from the closed areas are compensated for by increased recruitment to the open area. We note that the expected overall yield from the open area can be written as the product of the recruitment and the yield per recruit in that area. The overall recruitment gain will offset the yield loss from the closed area when the following condition holds:

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$$(15)\quad Y^{*}_{TOT} = \sum_{A\in OpenReserve} R^{*}_{A}(I)\mathrm{YPR}_{A}(I) \geq \sum_{A\in All} R_{A}(I)\mathrm{YPR}_{A}(I)$$

Note that the increase in expected recruitment in the open area is directly proportional to the ratio of total potential recruitment with and without the closure area, i.e., $R^{*}_{A}(I) = R_{A}(I)[R^{*}_{T}/R_{T}]$. With a little algebra it can be shown that the necessary increase in egg production must exceed the ratio of total yield from the entire area to the yield from the remaining open area. Thus the closed area will lead to increased total yield as long as

$$(16)\quad \frac{R^{*}_{T}(I)}{R_{T}(I)} \geq \frac{\sum_{A\in All} R_{A}(I)\mathrm{YPR}_{A}(I)}{\sum_{A\in OpenReserve} R^{*}_{A}(I)\mathrm{YPR}_{A}(I)}$$

A second condition for an improvement in total yield is that the magnitude of fishing effort in the remaining open areas must not increase. Displaced effort that would have otherwise been applied in the reserve area must either be eliminated or curtailed by regulation.

These two conditions for improvements in yield are restrictive and only address the potential gains in yield from permanent closures. If the magnitude of increase in total recruitment from closed areas is large, then it may be possible to make substantial long-term gains in yield from a network of relatively small but carefully spaced closure areas. Identification of these areas would be facilitated by consideration of hydrodynamic flow models in which the "reproductive footprint" of each area could be estimated. Early work by Tremblay et al. (1994) and recent advances (see Werner et al. 2001) hold considerable promise for identification of permanent reserve areas.

Discussion

We have demonstrated through simple models and examples that the spatial aspects of scallop biology and scallop distribution are essential considerations for the development of appropriate biological reference points and management policies to prevent overfishing in sedentary, aggregated species. Results from the spatial model for growth suggest that growth overfishing could be avoided by concentrating fishing in the lower productivity areas. Redirection of effort to areas of lower density may satisfy biological objectives, but the economic and social consequences of such measures may be difficult to justify. Harvests of scallops from low-density areas may also entail more extensive fishing effort with concomitant impacts on habitat, finfish bycatch, and contact damage to unharvested scallops.

Rather than focusing on yield maximization, we suggest an emphasis on the avoidance of recruitment overfishing. Our basin model results show that typical "boom and bust" effects, often attributed to environmental factors, can also be explained by spatial variations in habitat quality, spatial concentration of fisheries, dispersal of larvae among areas, and trends in mean size of the scallops. Results suggest that incentives to concentrate fishing effort in lower productivity areas may be an effective tool for reducing recruitment variation and improving yields. Reduction of fishing in the optimal habitats ensures that the reproductive capacity of the resource remains high.

Reductions in fishing mortality might be possible with closed areas as they can be used to reduce the concentration of effort on high scallop densities. Closure areas, however, can ameliorate but cannot solve the problem of excess fishing capacity. Rapid increases in stock biomass in the US Georges Bank closed areas have highlighted the problems of spatial averaging of fishing mortality (see Hart 2003). When fishing mortality is defined as a function of the total landings divided by the sum of biomasses in the open and closed area, two perverse outcomes are evident. First, low landings from the open areas are interpreted as evidence of low fishing mortality on the resource when, in fact, the open area could be seriously overfished. Second, the sum of biomasses in the open and closed areas may be sufficient to exceed the target biomass levels for the resource as a whole. Although this determination may be useful as a means of preventing recruitment overfishing, it can result in a fishery with landings well below the putative yields associated with biomasses near the target biomass at maximum sustainable yield (MSY).

Long-term improvements in overall recruitment are desirable but may not be achievable if the two conditions identified earlier are not satisfied. Rotational fishing areas, rather than permanent closures, may offer a solution that has less restrictive implications for the fishery. Two recent papers (Myers et al. 2000; Hart 2003) address rotational harvest policies for sea scallop populations. Both papers build on the cornerstone of yield per recruit from Beverton and Holt (1957) and the spatial extension by Caddy (1975). Hart (2003) introduced the concept of temporal averaging of fishing mortality rate as a way of addressing the appropriate optimum level of fishing mortality in areas that have been closed for a number of years. Caddy and Hart's results suggest that closures of 3 years or more are appropriate, 6 years are about optimal, and longer closures have diminishing returns for yield. The three areas on Georges Bank that have been closed since December 1994 could provide relevant information on the long-term empirical effects of closures on both the equilibrium biomass for an unfished population and the potential egg production. Efforts to develop rotational fishing policies in US fisheries are well developed, but actual implementation of such policies is likely to be several years away.

Our analyses and examples suggest that new technologies can be useful in the formulation of management policies that reduce the likelihood of recruitment overfishing, increase yield per recruit, and reduce its variability. Vessel monitoring systems can be used to identify productivity zones, monitor removal rates, and evaluate the potential consequences of displaced fishing effort. Information from acoustic multibeam mapping of habitat has been demonstrated as a means of improving scallop catch rates (Kostylev et al. 2003). Such systems can also be used to evaluate potential impacts of fishing effort on habitat and bycatch. However, such information can also lead to much higher rates of fishing mortality and possibly recruitment overfishing. As Caddy and Seijo (1998) noted, management systems must be designed to properly utilize information. Even quota systems are vulner-

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able to overfishing unless relatively precise fishery-independent abundance data can be obtained.

Perhaps the greatest gains for future management will come from the monitoring of closed areas, experimental fishing within such zones, and the development of appropriate modelling procedures for data so derived. Initial management experiments with rotational fishery policies have been informative. Rotational area management strategies offer the promise of balancing demands for increased yield, prevention of recruitment overfishing, maintaining spawning reserves, and reducing habitat damage and bycatch. Studies on Georges Bank and elsewhere may provide the best vision yet of the productive capacity of the sea scallop resource and the economic benefits derived from it.

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PERSPECTIVE / PERSPECTIVE

Precaution in the harvest of Methuselah's clams — the difficulty of getting timely feedback from slow-paced dynamics[1]

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Abstract: Geoduck (*Panopea abrupta*) stocks are perceived as stable and their fisheries as sustainable, but this may reflect a mismatch between slow-paced dynamics (maximum recorded age 168 years) and short-term perception. Management is based on biological reference points, whose appropriateness as a means to ensure sustainability is limited by a sedentary lifestyle and long-term trends in productivity. Analysis of age frequency distributions for 1979–1983, postharvest recovery rates measured in Washington in tracts pulse-fished during the 1980s and 1990s, and age frequency distributions compiled in British Columbia during the 1990s consistently suggest that recruitment declined for decades (long before the onset of the fishery), reaching a minimum around 1975, and rebounded afterwards. In such scenario, reliance on biological-reference-point-based harvest rules without timely feedback could accelerate population declines, eventually driving an apparently sustainable fishery to collapse. The merits of approaches that rely on monitoring and feedback using data-driven decision rules are stressed. Transition from a biological-reference-point-based strategy to one based on monitoring and feedback will demand a shift in research focus to the design of practical monitoring programs and the evaluation of management procedures by means of simulations. For geoducks and other long-lived organisms, monitoring should integrate data informative at different temporal scales.

Résumé : Les stocks de panopes du Pacifique (*Panopea abrupta*) sont perçus comme stables et leur pêche comme durable, mais il peut s'agir d'une discordance entre leur dynamique très lente (âge maximal enregistré de 168 ans) et notre perception à court terme. La gestion se base sur les points de référence biologiques dont la pertinence pour le maintien de la durabilité de la pêche est limitée à cause du mode de vie sédentaire de l'animal et des tendances à long terme de sa productivité. Des analyses des répartitions de fréquence des âges en 1979–1983, des taux de récupération après la récolte mesurés dans des zones soumises à la pêche périodique durant les années 1980 et 1990 dans l'état de Washington et des analyses des répartitions de fréquence des âges compilés en Colombie-Britannique durant les années 1990 indiquent toutes de façon concordante que le recrutement a décliné pendant des décennies (bien avant le début de la pêche commerciale) pour atteindre un minimum vers 1975 et remonter ensuite. Dans un tel contexte, l'utilisation de règlements de récolte basés sur les points de référence biologiques sans rétroaction peut accélérer le déclin de la population et éventuellement causer l'effondrement d'une pêche en apparence durable. Nous mettons l'accent sur les approches qui se basent sur le suivi démographique et la rétroaction et qui utilisent des règles de décision basées sur les données. Le remplacement d'une stratégie basée sur les points de référence biologiques par une autre fondée sur le suivi et la rétroaction exigera une modification des orientations de recherche vers l'élaboration de plans de suivi démographique et l'évaluation des procédés de gestion à l'aide de simulations. Dans le cas des panopes et des autres organismes à vie très longue, le suivi doit intégrer les informations à différentes échelles temporelles.

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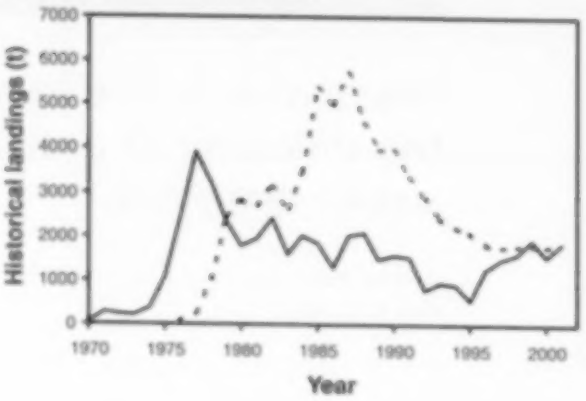
Introduction

Marine invertebrates of commercial value constitute a heterogeneous assemblage, confronting scientists and managers with a diverse array of peculiar problems (Orensanz and Jamieson 1998; Perry et al. 1999). Sedentary (not necessarily immobile) species with broadcast spawning, external fertilization, and pelagic larvae comprise a significant and well-defined subset of the assemblage that includes, among others, commercial bivalves. The assessment and management of these sedentary stocks present very specific difficulties mostly associated with the spatial structure of populations at different scales. Geoducks (*Panopea abrupta*) have an additional idiosyncrasy: they are extremely long-lived (Shaul and Goodwin 1982). Once a geoduck settles and buries itself into the substrate, it stays in place for up to 168 years (Bureau et al. 2002).

Harvested in subtidal grounds by commercial divers, geoducks support one of the most profitable fisheries in the northeastern Pacific from southeast Alaska to the Puget Sound Basin, Washington. Landings from the Washington and British Columbia fisheries (Fig. 1) constitute nearly all of the world's supply of this highly valued product. Interestingly, management systems differ radically between the two major fisheries: in Washington, geoducks on selected seabed tracts are auctioned yearly, while in British Columbia, there is limited entry and individual vessel quotas. In both cases, it is claimed that sustainability is ensured by very low harvest rates, on the order of 1%–3% of the harvestable biomass per year. The population dynamics of long-lived animals is necessarily slow paced, with the vagaries of recruitment and mortality being buffered by the coexistence of many year classes. At the time scale of the observation process, which is typically on an annual cycle, slow change in population structure conveys an impression of stability. When the annual survival of unharvested animals is on the order of 97%, stocks harvested at rates commensurate with natural mortality may secure a harvest for years into the future, even in the absence of recruitment. Given the observational errors typical in stock assessments, slow changes in abundance may not be readily detectable in survey data. This appearance of stability is further enhanced by hyperstability in the catch per unit of effort through the depletion process owing to shifts in the spatial allocation of effort (Hilborn and Walters 1992).

The sustainability of geoduck fisheries could be more apparent than real. Scenarios that could render the fishery unsustainable in the long run, even if harvest rates were low, include long-term declines in productivity, errors in the estimation of abundance, and (or) errors in the estimation of parameters commonly used to prescribe harvest rates. What would constitute a reasonable approach to manage these fisheries with precaution? In recent years, there has been a drive towards generic harvest control rules based on biological reference points (BRPs) (Restrepo et al. 1998). Mangel et al. (2002), in his synopsis of a symposium on "Targets, thresholds, and the burden of proof" (Coleman et al. 2002), listed species of limited mobility and long-term changes in productivity among situations that may render BRPs meaningless. Limited mobility is an intrinsic problem in the case of bivalves, and its implications have been discussed elsewhere (Orensanz and Jamieson 1998). The present study addresses the issue of slow-paced dynamics. Publicly available data (primarily age frequency distributions (AFDs)) are scrutinized to explore trends and patterns in recruitment. The merits of the assessment-based approach are discussed in light of the findings and alternative approaches that rely more on monitoring and feedback, using decision rules driven by data rather than mediated by models and assessments, are presented.

Fig. 1. Historical landings (tonnes (t)) in Washington (solid line) and British Columbia (broken line).



What kind of data would provide appropriate short-term feedback of value to management? AFDs reveal long-term trends in recruitment and abundance but they are not informative in the short term. Given the low rate of change of biomass, and considering uncertainty about the latter, surveys or ad hoc updates are unlikely to provide for timely feedback. One possibility would be a network of monitoring sites with variable histories of exploitation. As an example, results of an experiment conducted in Washington involving the monitoring of postharvest recovery at 15 sites are analyzed and discussed. This experiment received little attention in the past. The consistency between those results and results from analysis of AFDs is explored. It is argued that a narrow focus on BRPs leads management to overlook some significant phenomena evident in these data. The value of monitoring and feedback is emphasized and, in the particular case of long-lived organisms, the need identified to integrate pieces of information that are informative at different time scales.

Geoduck life history and its implications

Geoducks are extraordinary animals

Geoducks are extraordinary because of their size, lifestyle, growth pattern, and longevity. They are the largest infaunal bivalve in the world (individual weight up to 4+ kg) and live buried in the sediment down to a depth of approximately 1 m (Andersen 1971). Geoducks are dioecious broadcast spawners with pelagic larvae. The spawning season in Puget Sound runs between spring and early summer, peaking in June (Goodwin 1976); a single female may release millions of eggs during a spawning season. The pelagic larval stage lasts 25 days under hatchery conditions at 17 °C (Beattie

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and Goodwin 1993) but might extend longer in nature (up to 40–50 days). After settlement, postlarvae move at the sediment surface for several weeks (King 1986; Cole 1991) feeding on surface deposits until metamorphosis. Siphons then develop and suspension feeding begins while the juveniles bury themselves into the sediment. A technique to read internal rings in the hinge of the shells was first developed by Shaul and Goodwin (1982) and soon after utilized in several studies (Table 1). Geoducks have been convincingly shown to be extremely long-lived (Shaul and Goodwin 1982; Noakes and Campbell 1992; Strom 2002) with a recorded maximum age of 168 years (Bureau et al. 2002). Unlike trees and many deepwater fishes, geoducks grow fast during their first 7–12 years, and afterwards, their size remains virtually unchanged. On average, geoducks of 15 and 100 years of age do not differ significantly in weight (Breen and Shields 1983; Harbo et al. 1983; Bureau et al. 2002). Growth parameters for the von Bertalanffy model have been estimated in several studies (Noakes and Campbell 1992; Hoffmann et al. 2000; Bureau et al. 2002). Growth rate varies substantially along environmental gradients and between geographic regions (Goodwin and Pease 1991; Hoffmann et al. 2000; Bureau et al. 2002).

Given such longevity, natural mortality rates should be very low. Predation risk is very high during early benthic life (Goodwin and Shaul 1984) but decreases quickly after the age of 1 year (Sloan and Robinson 1984). Predation on adult geoducks has been generally considered rare under normal circumstances (Andersen 1971; Fyfe 1984). In recent years, however, predation by sea otters (*Enhydra lutris*) appears to have increased along the west coast of Vancouver Island, where the ranges of the two species overlap (Underwater Harvesters Association 2001). Published estimates of the coefficient of natural mortality (M) are in the range 0.014–0.054-year^{-1}.

The geoduck's lifestyle constrains monitoring, commercial harvesting techniques, and management options

The technique used to harvest geoducks is unique: commercial hookah-divers locate them by the tips of their siphons, which extend ("show") a few centimetres above the substrate, and then use hand-held water jets (stingers) to liquefy the sediment and extract the clams one at a time (for a description, see Washington Department of Fish and Wildlife (WDFW) and Washington Department of Natural Resources (WDNR) 1985). Orensanz et al. (2000), using data from Campbell et al. (1998), estimated a handling time of 0.3 min per geoduck, within the range of 0.25–0.5 min per geoduck indicated by WDFW and WDNR (1985). Once an adult geoduck is removed from the sediment, it cannot rebury itself; left on the bottom, it dies within a short period of time.

The vulnerability of geoducks to harvest gear depends on several factors: (*i*) the fraction of geoduck necks showing ("show factor") varies with sea conditions and is at a minimum during the winter (Goodwin 1977; Fyfe 1984), (*ii*) geoducks become available to commercial divers at ages between 4 and 12 years (Harbo et al. 1983), although for practical purposes, it can be assumed that they are fully recruited by an age of 8–10 years (Harbo et al. 1983;

Table 1. Published age frequency distributions of live geoduck samples from Washington and British Columbia with an indication of maximum recorded ages.

Site	Year(s)	Type of sample	Sample size	Maximum age (years)	Study
Puget Sound and Hood Canal (Washington)	1979–1982	11 unharvested sites, commercial gear	1 736	131	Goodwin and Shaul 1984
		3 unharvested sites, Venturi dredge	421		
Clayoquot Sound, west coast of Vancouver Island (British Columbia)	1980	Unharvested site, commercial gear	260	101	Fyfe 1984
Both coasts of Vancouver Island, five sites	1981	Harvested and unharvested sites, depletion of plots with commercial gear	2 276	126	Breen and Shields 1983
British Columbia (mostly west coast of Vancouver Island), eight landing sites	1981–1982	Commercial catch	1 396	146	Harbo et al. 1983
Hammond Bay near Nanaimo (British Columbia)	1982–1983	Commercial gear	365	107	Sloan and Robinson 1984
Ladysmith Harbour near Nanaimo	Nov.–Dec., 1980	Previously unharvested site, presumably commercial gear	403	102	Noakes and Campbell 1992
Near Gabriola Island (British Columbia)	1990	Presumably commercial gear	394	105	Noakes 1992
34 locations spread all over British Columbia waters	1993–2000	Savey samples, sites with diverse harvesting history, commercial gear	14 210	168	Bureau et al. 2002

Note: Noakes (1992) also reported the age frequency distribution of samples from Bamfield (his fig. 3A, n = 993) and Ladysmith (his fig. 3B, n = 847). It is not clear if the sample from Ladysmith used in the study by Noakes and Campbell (1992) (n = 403) is a subset of that reported by Noakes (1992).

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Bradbury et al. 1998; Bradbury and Taggart 2000), as shell factor and body size are not correlated for adults, (*iii*) harvest success is lower in shelly or compacted sediments, and (*iv*) visibility, often decreased by divers themselves because of sediment disturbance, can have an impact on harvest success. More important in determining the selectivity of the harvest are the factors that control the spatial allocation of effort (Campbell et al. 1998). Geographic gradients of density, size, and meat color are well documented and known to fishers, and so market preferences translate into patterns of spatial effort allocation. The proximity to port was an important factor during the early years of the fishery, particularly in British Columbia, leading to a gradual expansion from south to north (Campbell et al. 1998). As well, there are areas closed to harvest because of contaminated water, parks, etc., and deepwater areas that are beyond the operational reach of divers.

Because divers cannot determine the size of a geoduck before pulling it from the sediment, size limits are not a viable management measure. In Washington, meat color and price are correlated (the lighter the better) but color (as size) cannot be assessed until a geoduck is removed from the sediment. This introduces the possibility of high-grading, which occurs largely underwater as geoducks of poor quality are discarded in situ, creating serious problems for the assessment of the stock and the management of the fishery.

The dynamics of geoduck populations are poorly understood

Stocks are structured as metapopulations, collections of subpopulations of sedentary adults connected with each other by means of the dispersal of planktonic larvae. Relatively small segments of populations (not necessarily discrete, typically with an area of 20–50 ha) are defined as "tracts" in Washington or "beds" in British Columbia. In Washington, Sizemore et al. (1998) listed 267 tracts covering approximately 11 940 ha in total (average tract area is about 45 ha). In British Columbia, the fishing grounds are partitioned into geoduck management areas, of which currently there are a total of 243. Each geoduck management area comprises a variable number of beds. The estimated total bed area is close to 25 200 ha (Hand et al. 1998, their table 12), with an approximate mean bed area of 22 ha. No serious effort has been made to group beds into metapopulations, although some stocks (e.g., Hood Canal or southern Puget Sound) may correspond to metapopulation-level units. Any segment of such benthic metapopulations is open to recruitment by larvae originating at other beds. Availability of new settlers depends on local conditions prevalent in other regions as well as larger-scale environmental conditions that affect spawning and advection and survival of larvae. There is virtually no connection between the reproductive contribution of a given site and recruitment to that site. Pre- and postdispersal phenomena are decoupled, with the result that key processes in the dynamics may be completely blurred if analyzed at the wrong spatial scale.

As is the case with most benthic sedentary organisms, density dependence in geoduck metapopulations is likely to be significant only during benthic stages. Density-dependent interactions have small operational scales, as individuals are influenced only by their neighbors (Orensanz et al. 1998). The effects of localized (small-scale) density dependence on the dynamics of the metapopulation are mediated by larval dispersal. Thus, it is convenient to distinguish between pre- and post-dispersal density-dependent mechanisms (Botsford and Hobbs 1995) and whether these are compensatory or depensatory. In the two latter, survival and (or) per capita reproductive contribution respectively decrease or increase as density increases. Several types of processes have been invoked for benthic sedentary invertebrates with broadcast spawning, external fertilization, and pelagic larvae (Fig. 2). Predispersal density-dependent processes may affect reproductive output either directly through direct depensatory effects (e.g., low adult density results in poor fertilization success, the "Allee effect") or indirectly through compensatory effects (e.g., low adult density results in faster individual growth and higher reproductive output). These processes may be important depending on the concentration profile of the populations, which summarizes the density conditions experienced by individuals (second-order properties of the spatial process; Orensanz et al. 1998). Postdispersal processes may affect the rate of recruitment through the effect of resident density on larval settlement and survival of prerecruits. In the case of geoduck populations, there is no clear evidence of density dependence either pre- or post-dispersal. Although density-dependent growth has occasionally been invoked (e.g., WDFW and WDNR 1985), several inquiries (Breen and Shields 1983; Fyfe 1984; Goodwin and Pease 1991) have been inconclusive. Depensatory effects on fertilization rate, although likely given geoduck's sedentary habits, also remain undocumented. As for postdispersal density dependence, no evidence exists that high density of resident geoducks inhibits settlement rate, growth, and (or) survival of postlarvae and juveniles. Also, experiments conducted to evaluate the hypothesis that larval settlement is facilitated in the vicinity of adult siphons (whether due to chemical attraction or hydrodynamics-mediated mechanisms) were inconclusive (Fyfe 1984; Goodwin and Shaul 1984).

The dynamic response of geoduck beds to fishing remains virtually unknown. There is only scant information available on postharvest recruitment, all pertaining to postdispersal dynamics (Table 2). A few purposeful experiments were conducted by Goodwin and Shaul (1984), but results were inconclusive because of problems with design, logistics, and low natural recruitment. Interestingly, whatever information is available has been interpreted in support of two radically different hypotheses. Hypothesis 1 ("negative" effects): "The decreased number of juveniles in the fished beds is probably due to an adverse effect of fishing on recruitment. The low number of juveniles 1–3 years age group was probably due to lower post-harvest recruitment, suggesting that commercial geoduck fishing has an adverse effect on recruitment" (Goodwin and Shaul 1984, p. 14). Hypothesis 2 ("positive" effects): "There have been recent reports from commercial fishers of high proportions of juveniles in some beds that have been heavily fished in the past. This is substantiated by some aged biological samples taken during surveys" (Hand et al. 1998, p. 17). Hypothesis 1 is empirically substantiated by the recurrent observation of juveniles dislodged from the sediment during harvest operations (Goodwin and Shaul 1984). The significance of this effect has not been measured; juvenile geoducks are able to rebury themselves (Goodwin

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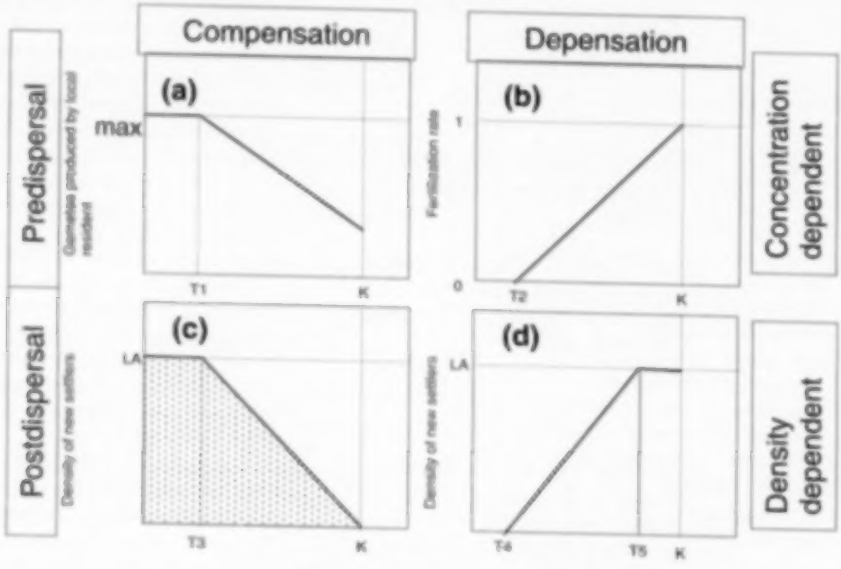
Fig. 2. Basic forms of density dependence documented or hypothesized for sedentary benthic invertebrates with broadcast spawning and pelagic larvae. Notice that in Fig. 2*c*, the solid line represents an "envelope" indicating the maximum density of new settlers expected for a given density of residents. In all others, the solid line corresponds to the expected value (mean) of the response variable, conditioned on the density of resident adults. *K*, local carrying capacity; *T1*–*T5*, density threshold levels; LA, index of larval availability; max, maximum of an index of relative gamete production by an individual.



and Pease 1989). Other ecological side effects of geoduck fishing are generally regarded as minor (Goodwin 1978; Breen and Shields 1983). Notice that environmental deterioration, incidental juvenile mortality, and postdispersal depensation could be confounded in experimental results. Hypothesis 2 is intuitively appealing. Adults are found aggregated in dense beds and have tremendous reproductive potential: millions of larvae are produced per capita during each reproductive season. Local (small-scale) abundance in such populations could be regulated through compensatory postdispersal density dependence; a virtually unlimited supply of prospective settlers would be regularly available to fill in gaps created by mortality of residents in crowded beds. Using closed-population stock–recruitment relationships as a metaphor, these are situations in which steepness is high: few breeders can quickly saturate a population decimated by mortality (e.g., by fishing) as long as aggregations exist to ensure successful fertilization. The implications for management are obvious and far-reaching. Recovery of harvested patches could be slow under Hypothesis 1, with a consequent reduction in productivity. Under Hypothesis 2, and considering that geoducks virtually stop growing after the age of 10 years, sustainable harvest rate could be possibly higher than dictated by rules of thumb based on natural mortality.

Postdispersal dynamics aside, fishing could pervasively increase predispersal depensation, even if this effect were practically undetectable. In sedentary broadcast spawners, the reproductive contribution of the stock may depend heavily on dense patches, but it is precisely there that fishers selectively allocate effort. As a bed or tract is depleted, there is, besides the obvious change in overall density, a less apparent effect on the spatial pattern of distribution (i.e., concentration or distribution of organisms relative to each other; Orensanz et al. 1998), with consequences on predispersal density-dependent processes.

Two contrasting management systems

The management systems in place in British Columbia and Washington are radically different, and so are their implications for the dynamics of the harvested stocks under different hypotheses about density dependence, in spite of harvest rate being very low in both cases. Summing up the contrasts, Freeman (1984) wrote that "British Columbia manages the geoduck like a fish, Washington like a tree. Both methods are controversial."

In British Columbia, the fishery is managed through a combination of limited entry and individual quotas (Muse 1998; Heizer 2000). The annual quota is set at 1% of virgin biomass (B_0), the long-term goal being to harvest 50% of B_0 over a 50-year horizon. Only a license was required during the earlier years. The number of licenses grew fast to a maximum of 101 in 1979, when a moratorium was introduced and licenses were made nontransferable. Between 1980 and 1981, the moratorium evolved into a formal limited entry program, with the number of licenses reduced to 55. Licenses, held by vessel owners, were made transferable between vessels but not between persons. Starting in 1989, the total quota has been split into equal parts among license owners, as requested by the Underwater Harvesters Association, the goal being "even distribution of the catch". Provin-

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Table 2. Hypotheses proposed to explain the local effects of the harvest on postharvest trends in recruitment rate and supporting evidence.

Hypothesis	Recruitment trends expected under hypothesis	Existing evidence
No effect	Same recruitment trends in harvested and unharvested plots	Inconsistent with the repeated direct observation of juveniles being dislodged from the sediment by harvesting operations; inconsistent with observation of higher density of prerecruits in unharvested plots than in harvested ones of the same tracts (Goodwin and Shaul (1984), their experiment 3)
Postdispersal overcompensation	Recruitment rate high immediately after harvesting and then gradually decreasing	No experimental evidence of postdispersal compensation; if observed, declining recruitment rate after the harvest could be confounded with global declining trends
Postdispersal depensation	Negative effect of removal of resident adults, settlement–recruitment improves as the adult resident population builds up	Consistent with positive correlation between number of adults left by the harvest and recovery rate in a recovery experiment (Orensanz et al. 2000); suggested by recurrently observed aggregation of juveniles in the vicinity of adults; enhanced survival consistent with experimental results on survival of planted juveniles (Goodwin and Shaul 1984, their experiment 4)
Incidental mortality	Recruitment drops after the harvest because of the incidental mortality of juveniles and then recovers as postharvest settlers start reaching harvestable size	Indicated by the repeated direct observation of juveniles being dislodged from the sediment by the harvest; presumably exacerbated by the tendency of juveniles to occur in the vicinity of adults (*e.g.*, Goodwin and Shaul 1984, their experiment 5); for that reason, consistent with positive correlation between number of adults left by the harvest and recovery rate in the recovery experiment
Environmental impact	Gradual increase in recruitment rate after "healing" of the substrate from disturbance caused by the harvest	Inconsistent with lack of correlation between number of clams harvested (an index of disturbance) and recovery rate in a recovery experiment (Orensanz et al. 2000); inconsistent with repeated demonstration of moderate ecological effects of harvesting; experimental results inconclusive (Goodwin and Shaul 1984, their experiment 6)

Note: Only hypotheses involving local-scale processes are listed. Recruits include preharvest resident juveniles and postharvest new settlers. Owing to incidental juvenile mortality, recruitment rate will tend to increase over time following the harvest, even if settlement rate is constant and not affected.

cial waters are divided into three regions (north, central, and south) and each region into three subregions. Under a "three-year rotation time" introduced in 1989, one out of three subregions within each region is harvested every 3 years. The quota for that year is three times the calculated annual quota. The rationales for the 3-year rotation are purely logistic: easy monitoring, reduced number of landing ports, and concentration of the assessment effort. A so-called "amortization program" (in place since 1995) was motivated by the desire to compensate for high quotas in some areas that result from various factors (estimation errors among them). Annual quotas are adjusted (down) to evenly spread the remainder of $0.5B_0$ over time through the end of the 50-year horizon. Given the geographic extent of subregions, fishers have considerable freedom in the spatial allocation of effort. The management system now in place has been credited with reducing effort while increasing rent through improved product quality and access to new markets. In recent years, the fishery grew to become the major invertebrate fishery in the province; an all-time record of CDN$ 42.5 million was reached in 1995 (Hand et al. 1998).

A unique auction-based system is in place in Washington (Sizemore 2000; WDNR 2000*a*). Tracts are leased to private individuals or companies through a public auction. The State contracts to the highest responsible bidder and generally collects above 50% of the landed value; the average annual revenue to the State during the last decade has been approximately US$ 6.2 million. Before 1998, the nominal harvest rate in Washington was 2% of B_0. More recently, a constant harvest rate strategy based on $F_{40\%}$ was adopted (Bradbury et al. 1998; Bradbury and Tagart 2000); the current target harvest rate is set at 2.7% of the estimated current biomass. The allowable catch is calculated under the $F_{40\%}$ policy and then a group of tracts estimated to support an exploitable biomass in excess of that catch is selected and leased through the auctions. A preharvest survey is conducted in each tract and WDNR auctions close to approximately 80% of the estimated biomass; leasees typically do not harvest the

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entire amount because of economic and logistic constrains (e.g., catch per unit of effort dropping to a nonprofitable level). According to a "recovery proviso", a tract cannot be opened to the harvest until a survey indicates that it has recovered to preharvest conditions (WDNR 2000*a*). In principle, at least, this proviso should result in de facto rotation and spatial tracking of recovery rate, as fast-recovery tracts would be revisited more often than slow-recovery ones.

The contrast between the two strategies was early highlighted by Fyfe (1984): "In Washington State, with a smaller area to manage, the harvest concentrates within well-defined boundaries", while "in British Columbia the fishery is spread over the whole coast. The relative merits of an intensive harvest in discrete patches vs. a moderate harvest over large areas are presently unknown." Twenty years later these "relative merits", which relate to prevalent types of density dependence, remain unknown and unexplored.

Beyond low harvest rates and the spatially explicit elements of harvest strategies, perhaps the most significant component of the actual (albeit implicit) management system is a contingency: the existence of de facto reproductive refugia. The most obvious are beds located at depths beyond the reach of commercial divers and regions where density is below profitable thresholds. The known depth range of the species extends from the low intertidal zone to 110+ m (Jamison et al. 1984). At least in some locations, density increases gradually with depth down to at least the operational limit of surveys (25 m; Campbell et al. 1996) and commercial diving. Many tracts in Washington cannot be harvested, and they are not considered in quota calculations. Areas can be designated as noncommercial because of pollution, low density, small extension, substrate, land-use conflicts, navigation, depth (too deep or too shallow), proximity of shore, conflicts with conservation priorities (e.g., eelgrass beds or proximity of bald eagle nests), etc. The extent, distribution, and potential reproductive contribution of deep beds are unknown in the two fisheries. An approximate calculation by WDNR (2000*a*, 2000*b*) suggests that only one fourth of the total Puget Sound stock is considered as commercial biomass (the basis for allowable catch calculations).

Four important pieces of information

Much of the published literature on geoducks reports the results of surveys of abundance and estimation of growth and natural mortality parameters. Here, we focus on four pieces of information that are key to understanding the dynamics of harvested stocks but either have received little attention in the past or have become available only recently. AFDs of dead animals (Goodwin and Shaul 1984) and results from a network of monitored sites (Goodwin 1996; Bradbury et al. 1998) were never analyzed before; data summaries were published only in technical reports of little circulation. AFDs of live animals collected in 1979–1983 were published but only used to estimate natural mortality (Breen and Shields 1983; Goodwin and Shaul 1984; Sloan and Robinson 1984). AFDs from samples collected in 1993–2000 from British Columbia became available very recently (Bureau et al. 2002). Exploratory analyses and supporting information are contained in two recent technical reports. Orensanz et al. (2000) scrutinized publicly available information about the ecology and dynamics of geoduck populations in Washington and British Columbia before 2000. Bureau et al. (2002) presented results on age and growth in British Columbia populations, the first study of this type to be published in 20 years, and the largest ever (14 210 geoducks aged).

Natural mortality estimated from AFDs of dead individuals (Washington)

Most published estimates of natural mortality rate are based on catch-curve analysis of AFDs of animals collected alive between 1979 and 1982 (Table 1). In all cases, a constant coefficient of natural mortality (M) was estimated by fitting the exponential model to a range of ages selected ad hoc (Table 3). All of the AFDs used showed a remarkable scarcity of individuals younger than 20–30 years, a pattern that likely reflects low recruitment before the 1980s, as discussed later. Under such long-term trends in recruitment, estimates of M based on catch-curve analysis are likely to be strongly biased. The mortality rate of adult geoducks can also be assessed directly by tracking the fate of individuals whose location has been mapped in experimental plots (Fyfe 1984; Bradbury et al. 2000). Bradbury et al. (2000) reported results of an experiment (n = 1128 tagged individuals) in Hood Canal, Washington. Their estimated value of M (0.016·year^{-1}, 95% confidence interval 0.007–0.025·year^{-1}) is close to the lower end of catch-curve estimates. A third method, proposed by Orensanz et al. (2000), was utilized to estimate M. Goodwin and Shaul (1984, their fig. 6) collected dead shells from 1-m^2 quadrats at three locations with a Venturi dredge, which is reputed to be non-size-selective. Only paired shells of dead animals found in the upright position within the sediment were retained to prevent the possible bias introduced by shell transport. Goodwin and Shaul (1984) claimed that "geoduck shells remain in the substrate many years after the death of the clam", which is generally the case for thick-shelled infaunal bivalves. Thus

$$N_i = \sum_{a=i}^{A} n_a$$

where i and a index age, A is maximum age, n_a is the number of shells of age a in the sample, and N_i is the number of shells of individuals that died at age i or older (i.e., that lived at least to age i) should provide a schedule of average survival more reasonable than the AFD of live animals. Situations that might bias the pattern are nonstationarity in the survival schedule or an overwhelming contribution to the dead-shell pool by one or a few year classes that have still not vanished completely from the living population. The latter is unlikely in the case of geoducks because of high longevity and low recruitment rate. Simulation exercises confirmed that this method is robust to long-term trends in recruitment, our main concern. There are two main possible sources of bias. First, a bias could occur if the rate of decay of empty buried shells varied with the age of the individual at the time of death and, second, age specificity in the rates of mortality because of sources that result in empty shells left at the sediment surface after death. Goodwin and Shaul

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Table 3. Published estimates of the exponential coefficient of natural mortality (M), all based on catch-curve analysis.

Study	Low cutoff	High cutoff	Age interval for grouping the data (years)	Range of estimated M values (year^{-1})	Observations
Breen and Shields 1983	10	None	27	0.014–0.019	The sample from one location, deemed not interpretable, was excluded from the analysis
Sloan and Robinson 1984	0	None	5	0.035	
	21			0.084	
Noakes 1992	20–50	None	5	0.034–0.038	Based on data published by Breen and Shields (1983), Harbo et al. (1983), and Noakes and Campbell (1992)
Bradbury et al. 1998; Bradbury and Tagart 2000	28	98	1	0.0236	Based on data published by Goodwin and Shaul (1984)
Orensanz et al. 2000	20	90	1	0.036	

(1984) argued that most adult shells remain within the sediment after death. This is consistent with direct observation of M by Fyfe (1984). While stressed individuals may be preyed by starfish, their shells ending up at the sediment surface, this seems to be a comparatively rare phenomenon. Removal of whole animals (shells included) by predators has been well documented for juvenile (small) geoducks, whose burrows are comparatively short, but seems to be rare in adults. A low cutoff point of 5–10 years should be utilized to minimize these potential biases. The cumulative frequency distribution of the AFD of the dead-shell sample (n = 459) departs from linearity (Fig. 3); the latter would be expected under the exponential model. Mortality seems to increase with age, which is to be expected under most biologically reasonable models and noticeable in populations of long-lived organisms. Age-dependent survival can be modeled with the Weibull function

$$N(t) = N_0 e^{-\alpha t^{\beta}}$$

where α and β are parameters and t is the age of a cohort. The exponential model is a particular case of the Weibull model for $\beta = 1$. The Weibull model was fitted to the observed cumulative distributions (Fig. 3, left). Estimated parameters are $\hat{\alpha} = 0.00174 \cdot \text{year}^{-1}$ and $\hat{\beta} = 1.64$. The Weibull model provides a very good fit over the entire age range. The exponential model gives a reasonable approximation to average survival for the age range 20–90 years (Fig. 3, right). The estimated value of M (0.036-year^{-1}) is within the narrow range estimated by Noakes (1992) (Table 3) and also the median of all published estimates of M.

Trends in recruitment extracted from AFDs compiled between 1979 and 1983 (Washington and British Columbia)

In the absence of long-term survey data, the history of the stocks was reconstructed based on AFDs compiled in six studies conducted in Washington and British Columbia, mostly between 1979 and 1983 (n = 7251 geoducks aged) (Table 1; Fig. 4). Examination of these data showed a consistent pattern: age classes younger than (at least) 30 years appeared to be underrepresented. The pattern was the same in samples from harvested and unharvested sites in British Columbia (data from Breen and Shields 1983). Three hypotheses have been implicitly or explicitly advanced to explain this intriguing pattern: (1) gear selectivity, usually invoked in catch-curve analysis (Breen and Shields 1983; Noakes 1992), (2) highly variable and patchy recruitment: gaps in recruitment could simply reflect the vagaries of recruitment at single locations (Breen and Shields 1983; Goodwin and Shaul 1984), and (3) a declining trend in recruitment (Sloan and Robinson 1984; Bradbury et al. 1998; Bradbury and Tagart 2000).

Hypothesis 1 is not tenable given that age selectivity is unlikely for geoducks older than 4–10 years (Bradbury and Tagart 2000). Hypothesis 2 is inconsistent with the geographic coherence of the pattern. To scrutinize Hypothesis 3, a time series of relative year-class strength was computed by back-calculating relative abundance at age 5+ years for all of the age groups represented in each sample. In these backwards projections, the parameters estimated for the Weibull

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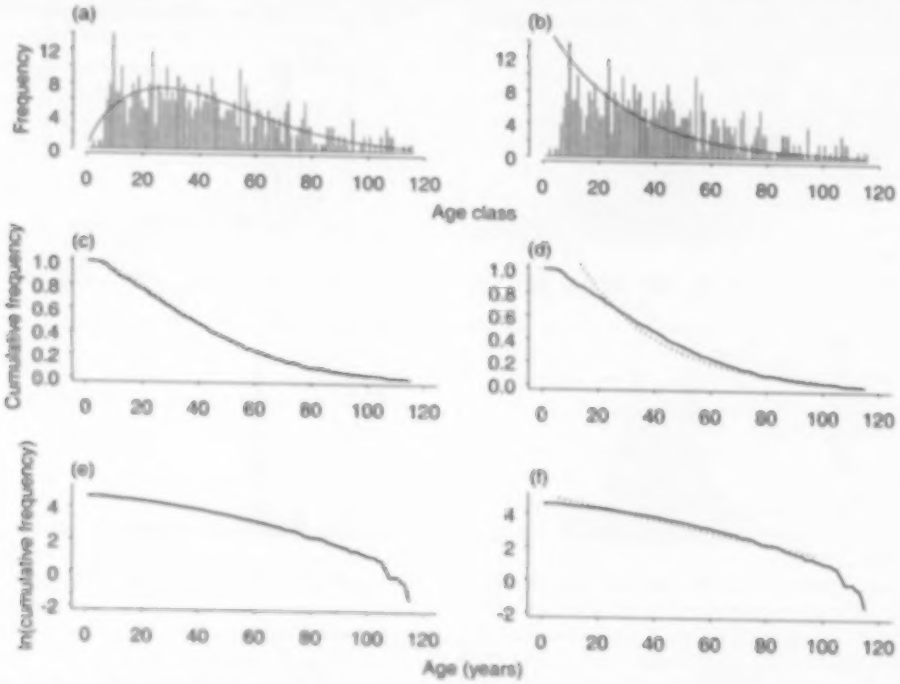
Fig. 3. Natural mortality estimated from samples of dead shell: (*a*, *c*, and *e*) Weibull distribution; (*b*, *d*, and *f*) exponential function; (*a* and *b*) age frequency distributions and model fit; (*c* and *d*) fit of the cumulative age frequency distribution by the two models; (*e* and *f*) log scale.



distribution were used. Time series of year-class strength back-calculated for the largest samples from Washington (Goodwin and Shaul 1984) and British Columbia (Breen and Shields 1983) show intriguingly coincidental patterns (Fig. 5). The rate of decline in year-class strength is comparable across these two large geographic domains, spanning five degrees of latitude (55–47°N) of intricate coastscapes. Most of the AFDs were obtained around 1980 and are thus indicative of a declining trend in annual recruitment rate during at least six decades (1920–1975) and at a large geographical scale. Consistently with Hypothesis 3, a generalized perception of very low and spatially variable recruitment rate (Goodwin 1976) discouraged direct observations of geoduck prerecruit abundance during the late 1970s.

Postharvest recovery in experimental plots (Washington)

This study was started during the early 1980s by Lynn Goodwin (WDFW). Fifteen tracts (Fig. 6*a*), due to be fished, were selected and sampled before the harvest, mostly between 1979 and 1985. Each site was revisited after the harvest (1.45–9.1 years after the preharvest survey) and again several years later (7–20 years after the first postharvest survey). Within each tract, a variable number of fixed stations (between 8 and 36) were established, each consisting of an 83.6-m^2 stripe. The total number of stations that were visited on the three occasions (all tracts pooled) was 324 (see Goodwin (1996) and Orensanz et al. (2000, their table 8) for complete information). Adult geoducks were surveyed visually (siphon counts) on each occasion.The experiment provided valuable information about fishing-related changes in abundance and the spatial pattern of abundance. At the time of the first postharvest survey, density (D_{post1}) was 5%–56% of the preharvest level (D_{pre}). After a few years of recovery, density observed during the second postharvest visit (D_{rec}) had increased in all the beds (Fig. 6*b*), attaining between 13% and 117% of the preharvest level. Close examination reveals the existence of two clusters of trajectories: a fast-recovery cluster (seven tracts), where average annual recovery rate ranged between 5.1 and 11.2 geoducks per plot, and a slow-recovery cluster (nine tracts), where average annual recovery rate was in the range of 1.0–2.6 geoducks per plot (Fig. 6*b*). Evidence of highly variable recovery rate in WDFW's experimental plots prompts the question of whether there is some identifiable environmental correlate. Goodwin (1990, p. 29) offered a clue: "in general, recruitment is higher in tracts where water currents are of medium velocity". Post hoc speculation about geographic patterns in the dynamics of recovery provides a basis to propose hypotheses about geographical gradients in recovery and recruitment rates. Recovery rate is a result of the balance between recruitment and mortality. Orensanz et al. (2000) analyzed the recovery process under the assumption that natural mortality is invariant across space, which would be justified if (as we believe is the case) geographic variation in recovery largely reflects variation in recruitment. Four models of recovery were considered, all dealing exclusively with postdispersal processes: constant recruitment rate, constant recovery rate (postulated by Goodwin (1996) and Bradbury et al. (1998)), pure compensation, and a sequence of depensatory and compensatory phases. In the latter three models, abundance was assumed to return to D_{pre}, where recruitment and natural mortality would balance each other. Such an assumption was

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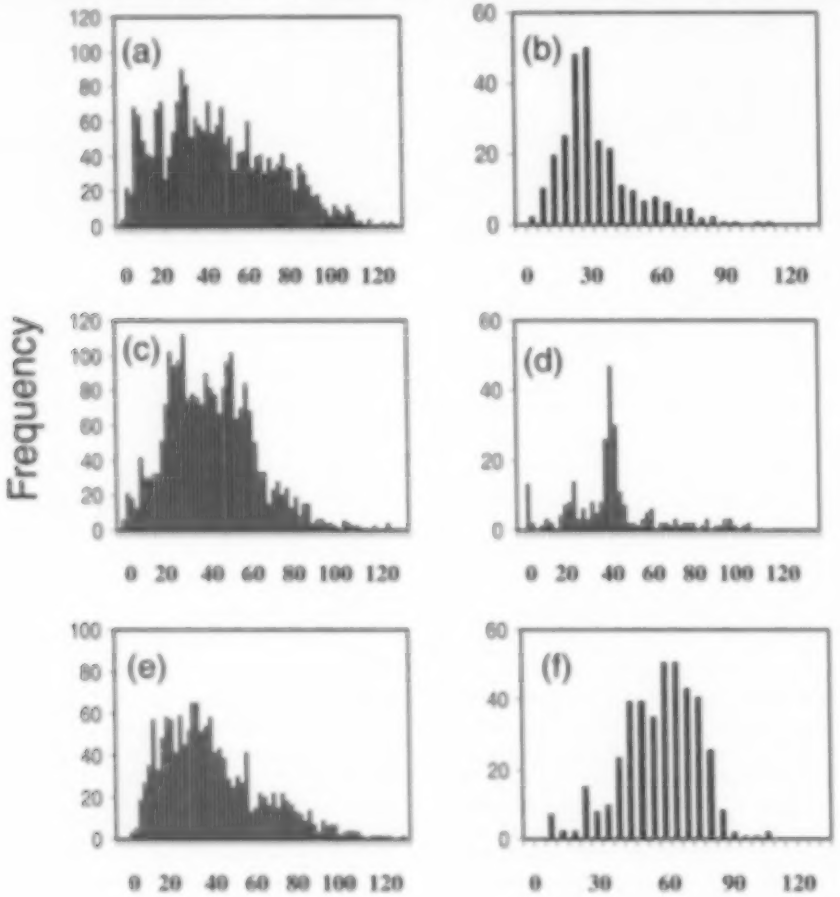
Fig. 4. Age frequency distributions published for Washington and British Columbia. The geographical level of aggregation is the highest used by the original authors. Interval widths are same as in original publications: (*a*) Goodwin and Shaul (1984); (*b*) Sloan and Robinson (1984); (*c*) Breen and Shields (1983); (*d*) Fyfe (1984); (*e*) Harbo et al. (1983); (*f*) Noakes and Campbell (1992).



not made in the constant recruitment model, which was therefore the most appropriate one to evaluate the rate of recruitment during the experiment relative to the preharvest condition. Under constant recruitment, the recovery trajectory is nonlinear and is described by

$$D_t = D_{post}e^{-Mt} + R\sum_{i=1}^{t} e^{-M(i-1)}$$

where R is the constant recruitment rate. There is no postdispersal density dependence, i.e., no inhibition or facilitation of recruitment by the resident population. Abundance increases asymptotically towards equilibrium, at which deaths are balanced by recruitment. A value of R was estimated for each site by forcing the trajectory to pass through D_{post} and D_{pre} and using a constant coefficient of natural mortality ($M = 0.035$-year^{-1}). The exponential model of survival, as discussed earlier, is a reasonable approximation for the range of ages expected to be represented in the population. Density in the slow-recovery cluster converges to D_{pre}, whereas in the fast-recovery cluster, it seems to converge towards a much higher level. Lower M, e.g., the value of M utilized by WDFW (0.0226-year^{-1}), results in even higher equilibrium density (D_{eq}). AFD data suggest decades of declining recruitment through the 1970s. Had this continued into the 1980s and 1990s, the recovery rates documented by WDFW would be inconsistent. Orensanz et al. (2000) scaled back-calculated trends of year-class strength to match D_{pre} levels observed in the recovery plots. Estimated annual recruitment rate was in the range of 0.013–0.049 recruits-m^{-2} in the slow-recovery cluster of plots and 0.071–0.150 recruits-m^{-2} in the fast-recovery cluster. On average, the recruitment rate estimated for the slow-recovery cluster is within the bounds expected from AFDs for the 1970s, whereas the rates estimated for the fast-recovery plots is comparable with recruitment levels back-calculated for the 1930s and

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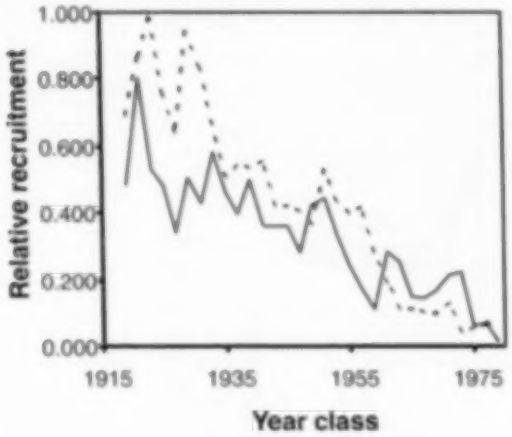
Fig. 5. Trends in relative recruitment (1915–1975) back-calculated from age frequency distributions from British Columbia (broken line) (data from Breen and Shields 1983) and Washington (solid line) (data from Goodwin and Shaul 1984) compared. The Weibull model of natural mortality was used in back-calculations.



the 1940s. This suggests that the low levels of recruitment calculated from AFDs for pre-1980 decades persisted during the 1970s in some regions, while recruitment may have rebounded to predecline levels in others. In no site did it decline further.

Concentration profiles were constructed to compare the spatial pattern of distribution of abundance between pre- and post-harvest surveys and between postharvest and post-recovery surveys (Fig. 7). The preharvest concentration profile corresponds to Type C of Orensanz et al. (1998) (equivalent to Type III of Prince and Hilborn 1998), which is typical of benthic invertebrate populations observed at scales on the order of one to several square metres and associated with hyperdepletion (i.e., abundance dropping faster than indicated by catch rate) in the fishing process. The postharvest profile corresponds to Type A (Type I of Prince and Hilborn 1998), which is typical of strongly thinned populations at the scale of observation. The fishery removed a substantial fraction of the geoducks, and those that survived the harvest were very "diluted" (Figs. 7*a*–7*d*). After a few years of recovery, the profile began converging back to Type C; as abundance increased, the absolute number of isolated individuals decreased (Figs. 7*e*–7*f*). The three cumulative profiles are compared in Fig. 8. The percentage of geoducks above the commercial threshold (as perceived at the spatial scale defined by quadrat size, which is not necessarily the perception scale of searching commercial divers) was 95% in the preharvest condition and then dropped to 65% after the harvest and rebounded to approximately 80% after some years of recovery.

Trends in recruitment extracted from AFDs compiled during the 1990s (British Columbia)

An extensive ageing project was conducted in British Columbia based on biological samples collected from 34 sites throughout the coast between 1993 and 2000 (Bureau et al. 2002). Those data were used to back-calculate year-class strength (cohort biomass at age 5 years) for each of the sites utilizing (*i*) the AFDs compiled by Bureau et al. (2002), (*ii*) estimates of B_0 (extracted from Department of Fisheries and Oceans reports), (*iii*) annual catch data for each bed (made available by the Department of Fisheries and Oceans), and (*iv*) a constant natural mortality coefficient of $M = 0.02 \cdot \text{year}^{-1}$. The latter is close to the experimental estimate of Bradbury et al. (2000) ($0.016 \cdot \text{year}^{-1}$) and to the value used by the WDFW ($0.0226 \cdot \text{year}^{-1}$). Simulation exercises showed that back-calculation of recruitment index series using the exponential model (with $M = 0.02 \cdot \text{year}^{-1}$) yields results that are very similar to those obtained with the parameters of the Weibull distribution, discussed earlier. To combine AFDs with catch data and estimates of B_0 (both reported in metric tons), biomass was assumed to be linearly related to numbers, which is justified by the fact that geoducks virtually stop growing in weight over the range of ages of interest (Bureau et al. 2002). Recruitment indices by site were pooled into six broad geographical areas to smooth out mesoscale spatial variation (Fig. 9). Because the samples were collected from different sites in different years, only samples collected in 1996 or later were used; only indices for 1996 and earlier year classes were included in the analyses (results are shown in Fig. 9).

Bureau et al. (2002) found indications that recruitment rebounded after 1980 in most regions, most notably in the south (west coast of Vancouver Island and Georgia Basin). The density of geoducks younger than 10 years was considered "significant" in comparison with estimated B_0. Good recruitment events appeared to have occurred during the 1980s and 1990s in beds with a wide range of harvest histories. The 1988 year class was particularly strong throughout the coast, but localized pulses of other year classes were also observed in all regions. That perception was confirmed by the back-calculated year-class strength analyses, which revealed some significant features (Fig. 9): year-class strength was at a global minimum around 1975 (indicated in Fig. 9 by a vertical broken line) and there was a post-1975 rebound in recruitment across all British Columbia coastal zones. The rebound occurred coherently in zones with very different harvest histories, reaching historical maximum levels along the west coast of Vancouver Island and the Georgia Basin (both heavily fished in recent decades). In the north coast and Queen Charlotte zones, which have been lightly fished, year-class strength shows a decades-long decline before 1975, a pattern comparable with that observed during the early 1980s in the south coast (Fig. 5). A comparable decline is not apparent in the data from Georgia Basin, the zone most heavily fished during the last two decades. The relatively strong rebound in this zone may indicate that effective harvest rate was higher than calculated, resulting in an underestimation of the relative strength of pre-1975 year classes.

An emerging large-scale pattern

Altogether, these four pieces of information are strongly suggestive of long-term trends in recruitment, coherent at a very large geographical scale. AFDs collected in 1979–1983 indicate that recruitment declined for decades, reaching a minimum around 1975. Pre- and post-harvest density data in several tracts in Puget Sound suggest a rebound in recruitment during the 1980s and early 1990s. The pattern that

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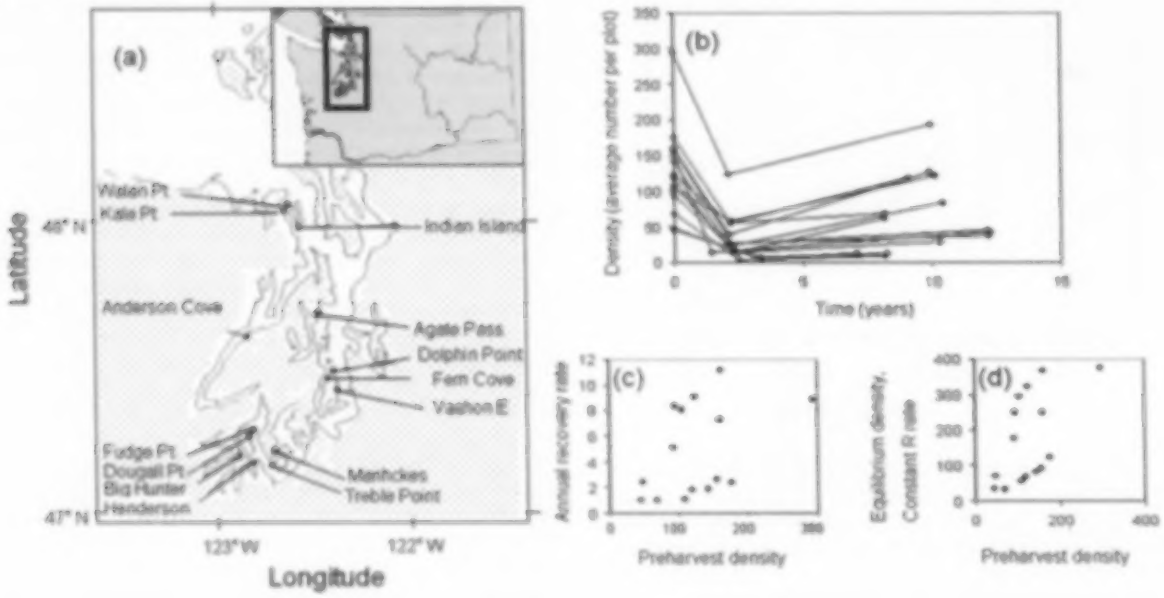
Fig. 6. (*a*) Puget Sound (inset map shows the location on the coast of Washington), sites of Washington Department of Fish and Wildlife's recovery experiment. Labeled on the right, fast-recovery cluster; labeled on the left, slow-recovery cluster. (*b*) Recovery in harvested plots; the three points correspond to mean preharvest, postharvest, and postrecovery densities. (*c*) Relationship between preharvest density and annual recovery rate. (*d*) Calculated equilibrium density reached under the constant recruitment hypothesis compared with preharvest density.



emerged from the AFDs compiled in British Columbia during the 1990s is consistent with that reconstruction of events. Preliminary results from Washington (J. Valero, unpublished data) indicate that strong recruitment pulses also occurred in the Puget Sound Basin during the last two decades, consistent with the geographic coherence documented for the pre-1980 decades.

BRPs are not appropriate as the sole basis for the sustainable harvest of geoduck stocks

Over recent years, there has been a drive in the United States and Canada towards generic harvest control rules based on target and limit BRPs proposed as default harvest guidelines that could perform adequately for most fisheries and circumstances (Restrepo et al. 1998). Generic harvest rules specify the desired harvest rate or catch as a function of the actual stock size, the case of the $F_{40\%}$ policy currently in place in the Washington geoduck fishery. Some BRPs are ad hoc rather than generic, as is the case for the $0.01B_0$ annual harvest rate implemented in the British Columbia fishery. For these harvest rules to work, the estimates of stock size must be reliable and BRPs must be well determined and meaningful in terms of the stock dynamics. Both conditions are difficult to meet in reality. Hilborn (2002) discussed some concerns with regard to the use of BRPs, among them the effect of uncertainty about virgin or actual biomass. This is a serious problem in geoduck stock assessment, as there is no expedient way of surveying geoducks over large areas. Current choices are either annual surveys of actual biomass in small areas to construct a composite map combining data collected over many years (Washington) or very coarse updates of estimated virgin biomass over broad areas (British Columbia). Details are provided in Appendix A. Uncertainty is high in the Washington case because estimated abundance is always outdated for large areas and in the British Columbia case because estimates are based on quantities (like bed area) that are even difficult to define. In British Columbia, for example, estimated B_0 went up during the early years of the fishery as new beds were discovered (Fig. 10) and then down as a result of a combination of lower estimates of density from survey data, arbitrary downscaling of area estimates, and bed boundary revisions. A later rebound of estimated B_0 was due to a combination of abandoning area downscaling, an increase in regional density estimates from surveys, a small increase in mean weight estimates, and some new beds found. Summing up, in neither of the two systems does this limited surveying capability provide adequate feedback about population trends, as required for the implementation of BRP-based harvest rules. Limited mobility and long-term changes in productivity, such as those found in geoduck stocks, bring to question the applicability of BRPs (Mangel et al. 2002; Parma 2002). Consider first the issue of spatial structure. In metapopulations of species of limited mobility, as discussed earlier, the decoupling of pre- and post-dispersal processes involved in stock–recruitment dynamics and the open nature of subpopulations preclude the use of simple stock–recruitment relationships. Yet, generic reference points, such as the $F_{40\%}$ utilized in Washington, have been proposed on the basis of their performance

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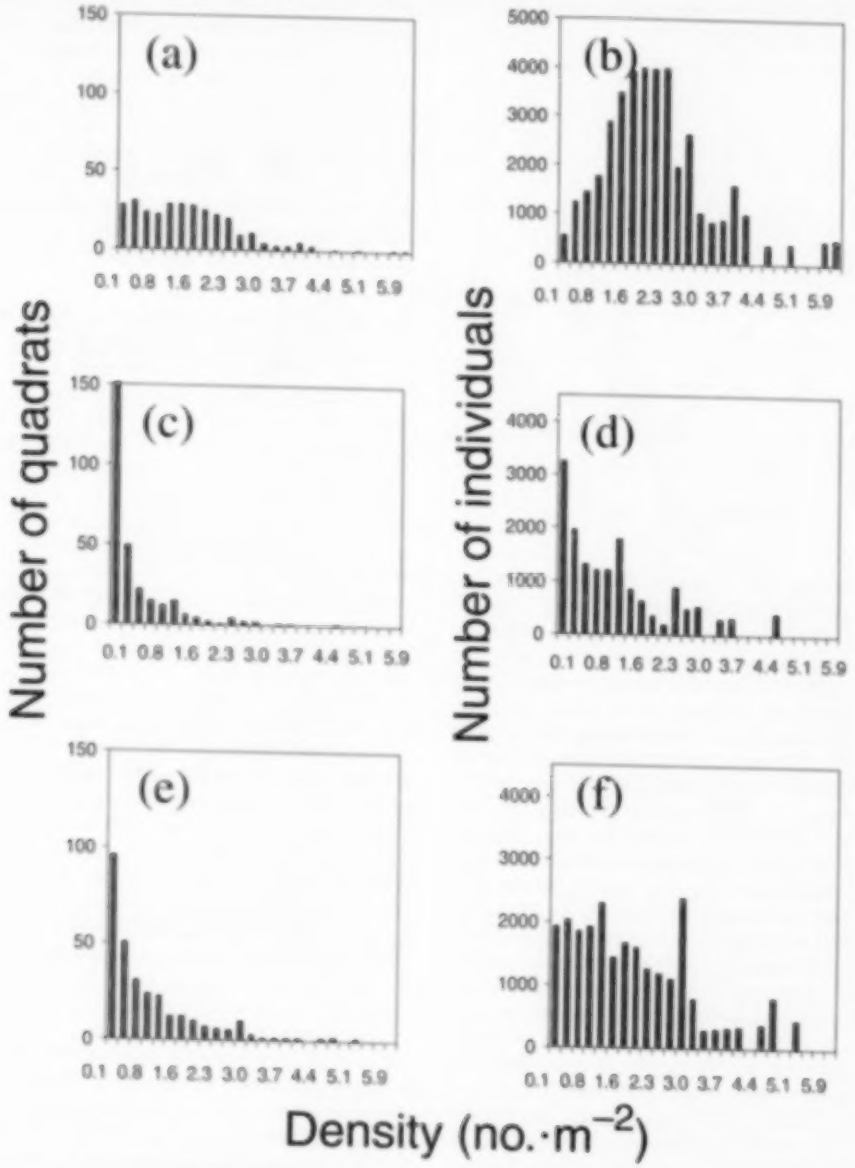
Fig. 7. Recovery sites (individual plots pooled): (*a*, *c*, and *e*) density frequency distributions; (*b*, *d*, and *f*) concentration profiles; (*a* and *b*) preharvest; (*c* and *d*) postharvest; (*e* and *f*) postrecovery.



evaluated using a range of stock–recruitment relationships under the closed-population assumption (Orensanz and Jamieson 1998). Significant elements of the renewal process, including connectivity and different forms of density dependence specified at the appropriate operating scale (Fig. 2), have never been properly incorporated into the evaluation of the strategies implemented in either fishery. The implications are not trivial. Recovery of harvested beds or tracts can be very different under the two management systems depending on the nature of density dependence. If concentration dependence of fertilization rate were significant, recruitment could depend on the reproductive contribution of high-density hotspots, precisely the ones that are selectively harvested by unconstrained fishers. This is illustrated by changes in concentration profiles produced by fishing in Washington's recovery experiment, described earlier (Figs. 7 and 8). A combination of concentration-dependent fertilization rate and fishers' freedom to allocate effort across large geographical areas would be a matter of concern in the British Columbia system. On the other side, if compensation were important, there would be a forgone productivity in a Washington-like system.

A second problem highlighted by Mangel et al. (2002) refers to long-term trends in productivity. Given the geoduck's extreme longevity, alleged stability of populations and sustainability of the fisheries that they support could possi-

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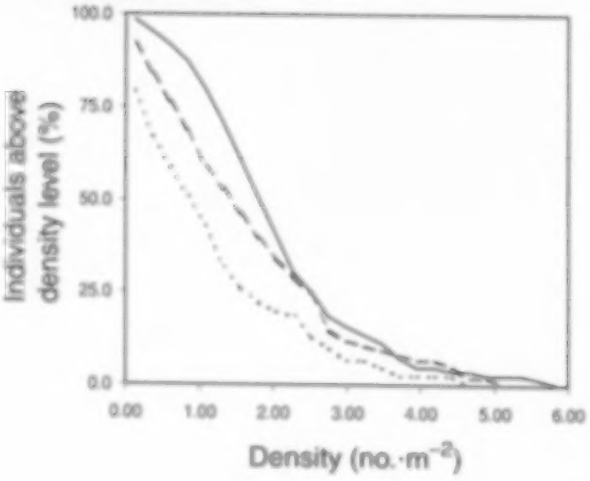
Fig. 8. Recovery sites (individual plots pooled): cumulative concentration profiles (percentage of individuals concentrated above density level): preharvest (solid line), postharvest (dotted line), and postrecovery (broken line) samples.



bly be more apparent than real. Geoduck abundance changes slowly, the impact of recruitment variability being buffered by the large number of year classes present in a population. Thus, eventual trends in abundance could be perceived only through the examination of long time series of data. Short-term variation in abundance is likely to go undetected because of large observation errors. Complicating things even further, and as is the case for other benthic fisheries, serial spatial allocation of fishing effort could result in hyperstable trends in catch per unit of effort underestimating the real rate of decline of total abundance. In fact, the large data set on catch and effort available in British Columbia has not been used in stock assessment for that reason. If the six-decade declining trend in recruitment detected in the AFDs from around 1980 had continued into the 1980s and 1990s, the application of BRP-based harvest rules without timely feedback could have accelerated the decline, eventually driving stocks to commercial extinction and an apparently sustainable fishery to a collapse. Nonstationary productivity also aggravates uncertainty about virgin biomass. Because geoduck fisheries started operating during the 1970s, biomass back-calculated to that period was used as an estimate of B_0. Back-calculation of relative abundance of geoducks in Washington based on AFDs suggests, however, that biomass in the 1970s was about 50% of the biomass during the 1920s and still declining, even in the absence of a fishery (Orensanz et al. 2000). As pointed out by Mangel et al. (2002) (after Hilborn 2002), virgin biomass is based on a theoretical construct that depends on existing environmental conditions.

The geoduck fishery started in 1970 in Washington and in 1976 in British Columbia and by 1980 was well developed in both jurisdictions. Since then, it evolved to become the most lucrative invertebrate fishery in the Pacific Northwest. Yet, evidence of a decades-long decline in recruitment ending around the mid-1970s and the rebound during the subsequent two decades went virtually unnoticed, this in spite of clear signs of the decline being present in AFDs collected between 1979 and 1983 and of stronger more recent recruitment in the results from Washington monitoring sites. A narrow focus on BRPs and BRP-based harvest rules had no use for information that did not contribute to the estimation of parameters required by standard models (B_0, M, K, L_∞). Once growth and mortality parameters became available, ageing efforts were interrupted for close to 20 years in both jurisdictions; Washington monitoring sites survived through the individual efforts of a few committed scientists. Distraction of scientists from important problems by narrowly focusing their attention on BRPs has been diagnosed as a general problem with this approach (Hilborn 2002).

An alternative approach, with emphasis on monitoring and feedback

Is there an alternative to the so-called "assessment-based approach" and reliance on BRPs? One worth considering emphasizes monitoring and feedback using decision rules driven by data rather than mediated by assessment models. In a "management-procedure approach", harvest regulations are driven by a predetermined feedback control rule, usually a simple algorithm for adjusting catches in response to monitoring indices. The possible outcomes of alternative management procedures are evaluated through simulation of the dynamics of the system (stock, fishery, and monitoring) with an operating model, tailored to specific situations (e.g., Butterworth and Punt 1999; Parma 2002). The operating model can be as complex and realistic as desired, but decision rules usually depend on simple calculations. The management-procedure approach appears as a reasonable option for the design of stock-specific harvesting strategies, which in the case of geoduck could include different sorts of spatially explicit regulations. While spatial components are present in both management systems (de facto reproductive reserves, even distribution of the harvest in British Columbia, de facto rotation in Washington), their merits, significance, and implications have never been evaluated. This management-procedure approach is currently being explored by some of us (J. Valero, A.M. Parma, and R. Hilborn); results will be reported elsewhere.

The question, now, is what kind of monitoring would be most appropriate in the case of geoduck fisheries. Monitoring may prove difficult in a situation where abundance changes at a very slow pace because of low rates of mortality (natural and fishing) and recruitment and complicated by the fact that actual abundance cannot be accurately surveyed every year over the entire region of interest. AFDs are informative about stock dynamics at a time scale far larger than that required for timely management response. Is there any practical way of complementing AFDs with information meaningful at a shorter time scale, more commensurate with the scale of management decisions? Given that short-term changes in total abundance are buffered by the coexistence of many year classes, and thus difficult to detect, a more proximate index of short-term recruitment success would be more suitable. A network of monitoring sites (plots) with variable histories of exploitation is a possibility, well exemplified by the experimental study of postharvest recovery described earlier. Such a network has several merits: (*i*) it is

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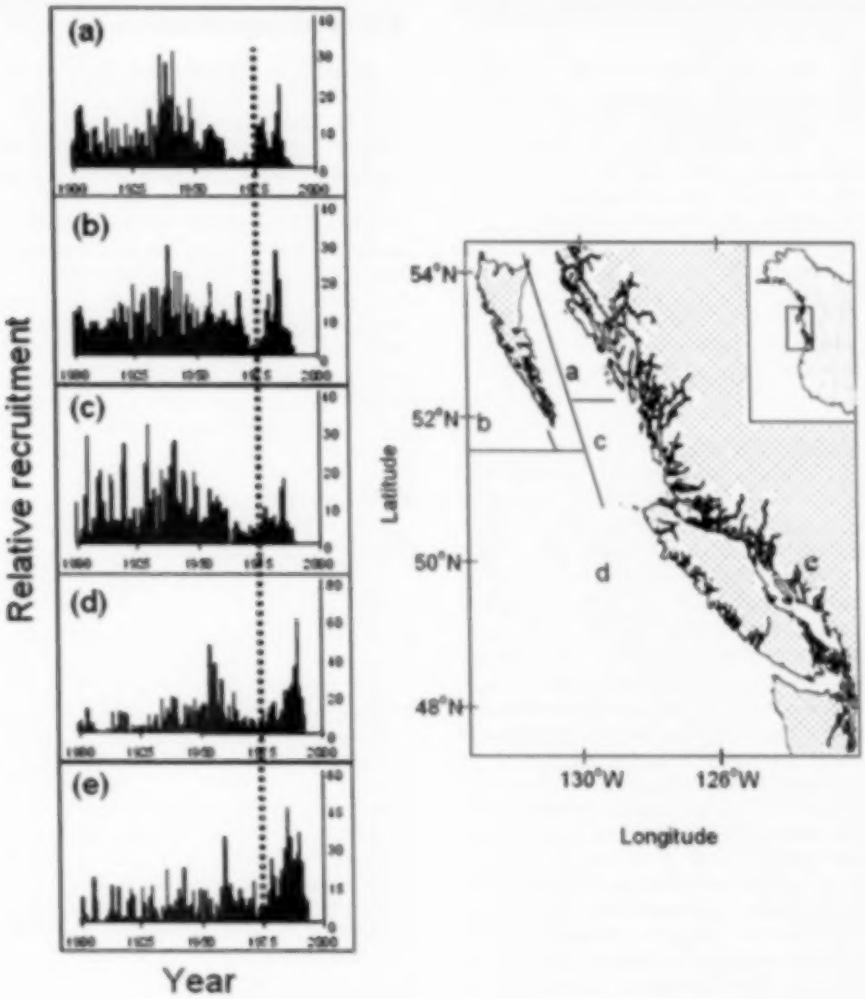
Fig. 9. Time series of relative recruitment backcalculated for five regions in British Columbia from age frequency distributions in Bureau et al. (2002): (*a*) north coast; (*b*) Queen Charlotte Islands; (*c*) central coast; (*d*) west coast of Vancouver Island; (*e*) Georgia Basin. See text for details.



informative about geographic and temporal patterns in recruitment, (*ii*) it may contribute to a better understanding of postdispersal density dependence and postharvest dynamics, and (*iii*) the data incorporate the effects of poaching.

As discussed earlier, results from Washington's experimental plots obtained during the 1980s and early 1990s appeared to be inconsistent with trends in recruitment reconstructed from AFDs compiled between 1979 and 1983. The age data that were needed to determine whether this was due to a rebound in recruitment became available only two decades later. First a worrisome sign, later the good news: both went unnoticed even when evident in the raw data. The consistency of results from AFDs and from experimental sites illustrates the value of integrating different pieces of information into a monitoring program to capture the dynamics of the harvested stock at different time scales. Yet, it is important to consider that information must be analyzed at a meaningful spatial scale. If long-term regional trends in recruitment are the subject of interest, then information has to be pooled at a large spatial scale to override the effect of small-scale spatial variability. If small-scale density-dependent processes are investigated, then experiments must be tuned to the operating scale of the phenomenon of interest (e.g., through the size of the experimental plots).

Beyond conservative harvest rates

The precautionary approach to fisheries management is often narrowly equated with the adoption of cautious harvest levels, guided by conservative BRPs (Restrepo et al. 1998). This emphasis is a result of fishery regulations articulated after the Sustainable Fisheries Act (in the United States), several international treaties, and other regulatory frameworks. BRPs, and their shortcomings, were discussed earlier in this paper in relation to geoduck fisheries. A well-known consultation conducted by the Food and Agriculture Organi-

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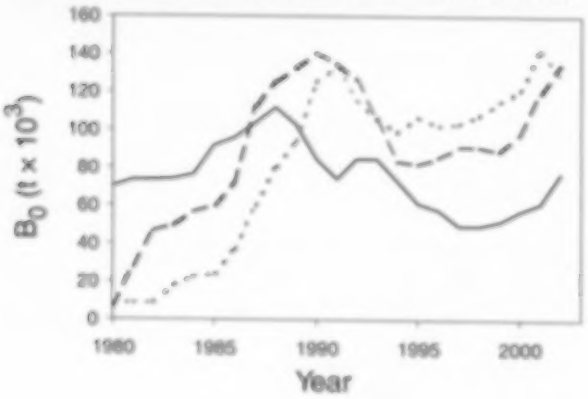
Fig. 10. Virgin biomass (B_0) calculated for three regions in British Columbia, 1980–2002: north coast (dotted line), west coast of Vancouver Island (broken line), and inside waters (solid line).



zation (1995) espoused a much broader view of the precautionary approach to fisheries management, emphasizing institutions, monitoring of the fishery, feedback on regulations, and effective implementation (Hilborn et al. 2001). Ultimately, the structural requisite for sustainability is a management system that offers appropriate incentives to managers, fishers, and other stakeholders. Those incentives take the form of tenure or long-term user rights. User rights are clearly defined in both fisheries, which should prevent the race for fish and overcapacity. The fisheries are not subsidized; instead, the fishery in Washington contributes significant revenues to the State, while in British Columbia, the industry covers the costs of sampling, surveying, and monitoring. Yet, there are significant challenges that still require continued attention, including conflicts between stakeholders, as exemplified by the restoration of rights to Native Americans or First Nations (Fangman et al. 1996), poaching, a problem common to all valuable species from coastal zones, and high-grading (low-quality dark geoducks left on the ground). The latter has been encouraged by the quota system in British Columbia and by uniform taxation of the catch in Washington. Enforcement alone has proved insufficient to deal with poaching and high-grading. These problems pertain mostly to the structure of the management system, institutional frameworks, tenure, and incentives.

The ultimate challenge for scientists and managers is the development of management strategies that rely on monitoring and well-designed indicators. The transition from a BRP-based strategy to one based on monitoring will demand a shift in research focus to the design of practical monitoring programs and the evaluation of management procedures by means of simulations. The simulation models need to represent the process of feedback as well as the dynamics of the resource and the fishing process, as regulated by management. The two different management systems in place in Washington and British Columbia have different monitoring demands: the first requires intensive surveying of tracts that are candidates to be opened and the second a protocol to assess stock status at larger spatial scales, with industry participation. In both cases, the strategies need to provide for timely feedback and thus be sensitive to the state of the resource at a range of time scales, which in the case of geoducks, is dictated by their extraordinary biology.

Acknowledgements

We wish to dedicate this study to Lynn Goodwin who, early on, identified all of the important issues on geoduck ecology and fisheries, solved many of them, and set the compass for future work. We enriched our understanding of geoducks and their fisheries through discussion with or criticism from Alex Bradbury, Bob Sizemore, and Lisa Veneroso (WDFW), Alan Campbell, Rick Harbo, and Steve Heizer (Fisheries and Oceans Canada, Nanaimo, British Columbia), Jamie Austin (Underwater Harvesters Association, British Columbia), David Fyfe (Northwest Indian Fisheries Commission, Suquamish, Washington), Steve Jennison and Doug Williams (WDNR), and Paul Breen (NIWA, New Zealand). Lobo's work was supported by project PIP-CONICET 0656/98 (Argentina) and by the School of Aquatic and Fishery Sciences, University of Washington.

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Appendix A

In Washington, the biomass of each tract is assessed through direct transect surveys conducted by Washington Department of Fish and Wildlife biologists (Bradbury et al. 1998). Only a limited number of tracts can be surveyed each year. For the others, the most recent estimate is used, subtracting the catches when fishing occurred after the last survey. No adjustments are made to account for natural mortality or recruitment, either separately or pooled, as a recovery rate factor. For a tract to open, a survey must have occurred within the previous 10 years; otherwise, a new survey is required.

Stock assessment in British Columbia is described in detail in Hand et al. (1998). Catch and effort data were initially collected through a mandatory logbook program implemented in 1977, but inconsistencies were found with port validation. This led, after 1996, to a program (funded by the industry) in which port monitors collect harvest information from fishers at the time of landing. Since catch per unit of effort is not accepted as a reliable index of abundance, catch and effort data are not used in stock assessment. Virgin biomass is calculated on a bed-by-bed basis as the product of three factors: bed area (which is acknowledged to be affected by significant mapping errors), virgin geoduck density estimated through direct transect surveys of some beds and extrapolated to unsurveyed beds, and mean geoduck weight.

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PERSPECTIVE / PERSPECTIVE

A hierarchical approach to determining reference points for Pandalid shrimp[1,2]

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Abstract: Reference points for harvesting Pandalid shrimp are categorized into five general approaches: historical proxies, biomass dynamics models, dynamic pool models, stock–recruit models, and demographic production models. Each of these approaches has different data requirements and underlying assumptions. Estimation of biological reference points from these methods can be viewed as a hierarchy, using data-poor proxies in the lowest tier to applying more informative demographic production models in the highest. Based on a review of Pandalid life histories, precautionary-approach reference points, and methodologies for estimating reference points and their applications to Pandalid shrimp stocks, we advocate a progression from proxies to more informative models and the requisite advancement of research programs to develop reliable reference points for Pandalid shrimp stocks.

Résumé : Les points de référence utilisés dans les pêches de crevettes pandalidées représentent cinq approches générales, soit les variables de remplacement historiques, les modèles de dynamique de la biomasse, les modèles dynamiques d'agrégation, les modèles stock–recrues et les modèles démographiques de production. Chacune de ces approches requiert des données différentes et possède des présuppositions sous-jacentes distinctes. L'estimation des points de référence biologiques au moyen de ces méthodes peut former un processus hiérarchique, l'utilisation des variables de remplacement pauvres en données formant l'échelon inférieur et celle des modèles démographiques de production l'échelon supérieur. Après avoir passé en revue les cycles biologiques des pandalidés, les points de référence basés sur le principe de précaution, les méthodologies pour estimer les points de référence et l'application des points de référence aux stocks de crevettes pandalidées, nous recommandons de suivre une progression depuis les variables de remplacement jusqu'aux modèles plus riches en information et de mettre au point les programmes de recherche nécessaires pour développer des points de référence fiables pour les pêches de crevettes pandalidées.

[Traduit par la Rédaction]

Introduction

Despite the unique challenges for modeling Pandalid shrimp populations, a variety of approaches have been applied to determine sustainable harvest rates or stock size thresholds. Reference points are used to determine the desirability of actions (e.g., a fishing mortality rate reference point to determine what rate is excessive) or the desirability of effects (e.g., a stock biomass reference point to determine a healthy stock size). Approaches range from simple descriptive proxies for "data-poor" applications to highly informative analytical estimates and from conventional fisheries models to innovative methods that account for the peculiarities of Pandalid life histories. Each approach has strengths and weaknesses for providing appropriate reference points for sustainable harvest. Therefore, the method of choice depends largely on the information available for each resource and fishery.

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[1]This paper is dedicated to the memory of Stephen H. Clark (1940–2004) and his many contributions to the science and management of Gulf of Maine shrimp.
[2]Derived from the Workshop on Reference Points for Invertebrate Fisheries, Halifax, Nova Scotia, 2–5 December 2002.
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Pandalid biology

The multidisciplinary nature of complex population modeling may pose a challenge to determining reference points for Pandalid shrimp. Balsiger (1981) in a keynote address at an international shrimp symposia illustrated the persistent challenges of assessing and managing shrimp stocks. He concluded that management failures have not been from a lack of conservation strategies, but from uncertainty in basic population parameters. Several aspects of Pandalid biology, such as environmental influences, complicated life histories,

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and trophic interactions, pose challenges to traditional fisheries modeling exercises and estimation of reference points.

Twelve species of Pandalid shrimp support commercial fisheries, and most species are distributed discontinuously throughout boreal waters of the North Atlantic, North Pacific, and Arctic oceans (Fox 1972). Pandalid shrimp in the Atlantic are dominated by *Pandalus borealis*, but Pacific resources have a wider diversity of Pandalid species (e.g., seven species of Pandalid shrimp are harvested in British Columbia shrimp fisheries and eight species are harvested in Alaskan fisheries). Pandalid shrimp occupy a number of different niches and habitats. Some species are benthic, some show nocturnal pelagic migrations, and some are generally pelagic in nature. They also occupy different habitats from rocky to sandy to green mud. They are found at depths ranging from intertidal tide pools to >1300 m. They are found in offshore regions to isolated populations in inshore inlets.

Distributions are principally determined by temperature, salinity, and bottom type (Haynes and Wigley 1969). Environmental factors also have profound influence on life histories within and among Pandalid populations (Nilssen and Hopkins 1991; Hansen and Aschan 2000; Koeller 2000). For example, ocean climate and ice cover have significant effects on population dynamics and fishery yields (e.g., Shumway et al. 1985; Hannah 1993; Tande et al. 1993). Boutillier and Joyce (1998) noted that, in British Columbia for the same species of shrimp, populations occupying the more environmentally dynamic open-water offshore areas showed larger fluctuations in population size than did isolated populations in sheltered inshore areas where the environmental conditions remain relatively stable. Anderson (2000) also pointed out that the environmental effects may be different for different species. For those species restricted to shallow, narrow depth ranges, environmental effects may be very large, whereas those species with deep, broad depth ranges may be able to compensate for environmental changes by changing their depth distribution.

One obvious challenge to applying conventional age-based assessment models is the absence of direct age determination techniques for crustaceans. Furthermore, application of length- or stage-based models is difficult because of complicated life histories affecting growth patterns. Growth is a discontinuous process and is associated with molting of the exoskeleton (Hartnoll 1982). The number of molts that an animal goes through in a year varies by age and life stage. Growth seems very rapid in the spring and summer and slows in the late summer and fall with the onset of gametogenesis. Egg-bearing females stop molting, but males resume growing after the fall–winter spawning season.

Pandalid shrimp are protandrous hermaphrodites. They normally spawn first as males and then go through transition to females (Bergström 2000), but some species have the ability to skip the male phase and mature directly as females. This later condition may be a compensatory mechanism for a population, lending resilience to stock collapse. Charnov (1982) discussed the adaptive advantages for an animal to become a primary female. This seems to occur when there is an imbalance between the number of males and the number of females, which can occur when a strong year class is present or when the older year classes have been overfished. Hannah and Jones (1991) reported on fishery-induced changes of increased growth rates and younger age structure of the *P. jordani* stocks off the coast of Oregon. The abundance of primary females increased when the age structure shifted to younger shrimp. The fishery originally exploited three year classes of shrimp but recently targeted virtually a single age class (age-1+ shrimp) composed of nearly 50% primary females. The ability of some species to accelerate sex change and growth rates was thought to make modeling the population of these animals very complex. It was initially thought that these compensatory mechanisms made these species very resistant to overharvesting; however, some recent work and trends in populations indicates otherwise (Hannah 1999).

In contrast to many marine species that broadcast gametes into the water column, Pandalid shrimp have internal fertilization, and females brood eggs on their pleopods until larvae are hatched (Balsiger 1981). Incubation periods also vary with temperature (Shumway et al. 1985). After hatching, Pandalid shrimp spend a portion of their lives as pelagic larvae. The number of stages and the morphology of the larvae vary considerably between species. The rate of development through these stages seems too be affected by environmental conditions such as temperature (Boutillier and Nguyen 1999). The amount of time that an animal spends in a pelagic larval stage and the degree of development, which affects their mobility in the pelagic zone, can in turn affect their distribution and contribution to a metapopulation. This can lead to some rather complex metapopulation stock–recruitment relationships (Hannah 1995; Boutillier et al. 1997).

Some Pandalid species form dense seasonal aggregations, which have large effects on fishery catch rates (Balsiger 1981). Perry et al. (1999) also found a significant correlation between short-term variations in catch per unit effort (CPUE) in the *P. jordani* fishery and environmental conditions such as wind stress, tidal current speed, sea surface temperature, salinity, and hours of bright sunshine. There are also known diel migrations both vertically and horizontally (deep to shallow waters), depending on the species (Barr and McBride 1967; Shumway et al. 1985; Boutillier and Sloan 1988), which have a significant effect when developing standardized fishery-dependent and -independent indices of abundance.

Pandalid shrimp can be considered a keystone component of boreal ecosystems, consuming zooplankton and other benthic organisms, including themselves. They are also preyed on by many demersal and benthic invertebrate and fish species (Butler 1980; Kurata 1981). For example, Shumway et al. (1985) report 14 fish species that rely on *P. borealis* as a major food source. Many traditional methods of single-species population modeling fail because of the large influence of predation rates and their variability on shrimp population dynamics (Jakobsson and Stefánsson 1998; Lilly et al. 2000; Berenboim et al. 2000).

Bo Bergstrom (summarized by Koeller et al. 2000*a*), in his keynote address at the 1999 International Symposium on Pandalid Shrimp Fisheries – Science and Management at the Millennium, noted a wide information gap between biologists and assessment scientists. Shrimp biologists tend to focus on the variability and complexity of Pandalid life histories, whereas population modelers tend to simplify the same processes and ignore abiotic influences. We advocate an inter-

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disciplinary approach to reference point estimation in which complex biological information is incorporated into models and sensitivity analyses identify critical model components to refine biological and fishery research programs. As is shown above, Pandalid shrimp have a number of compensatory biological traits that function at varying degrees depending on the species, the state of the population, and environmental conditions. These mechanisms affect the resilience of the population to perturbations such as fishing and need to be incorporated into the population production models. We suggest that models should be iteratively improved through feedback to field-sampling programs, as commonly practiced in quantitative ecology (e.g., Overton 1981).

The uncertainty paradox for Pandalid shrimp

A recent trend in fisheries management is the application of a precautionary approach (PA), which involves consideration of scientific uncertainty in decision making. Elements of the precautionary approach for fisheries management were first defined in a voluntary agreement, the Food and Agriculture Organization Code of Conduct for Responsible Fisheries (FAO 1995*a*), which was influential in effecting the widespread application of a precautionary approach for fisheries management. The FAO Code of Conduct states that "The absence of scientific information should not be used as a reason for postponing or failing to take conservation and management measures" (FAO 1995*a*). FAO's guidelines to the precautionary approach explain that reference points should be used to avoid overexploitation and quickly rebuild depleted stocks (FAO 1995*b*).

Over the last decade, many fisheries organizations have adopted some form of the precautionary approach, either in name or implicitly by adopting common PA elements. In 1995, the United Nations (UN) adopted PA in two binding fisheries agreements (Straddling Fish Stocks and Highly Migratory Fish Stocks Agreement and the Fishing Vessels on the High Seas Agreement, UN 1995). The Straddling Stocks Agreement states that "The fishing mortality rate which generates maximum sustainable yield should be regarded as a minimum standard for limit reference points". In conformance with the Code of Conduct, F_{MSY} was considered as a limit reference point, which is a considerable shift from the traditional view of maximum sustainable yield (MSY) as an objective (Mace 2001). Other intergovernmental organizations such as International Council for the Exploration of the Sea (ICES) and the Northwest Atlantic Fishing Organization (NAFO) soon followed the UN in explicitly adopting PA as a management strategy. In 1997, ICES and NAFO each developed a framework of limit reference points and precautionary targets (ICES 1997; Serchuk et al. 1997).

Despite the basic tenet of the precautionary approach that fishery management actions should be taken despite uncertainty, estimation of precautionary-approach reference points requires relatively informative stock assessments with a long time series of stock size, recruitment, and fishing mortality estimates that represent a wide dynamic range of stock conditions. Accordingly, less than half of management units that are regularly assessed by ICES and only one NAFO stock currently have precautionary-approach reference points for both F and stock size (ICES 2001; NAFO 2001). In particular, the limited information available for many Pandalid shrimp resources is not considered to be adequate for deriving precautionary-approach reference points. For example, none of the four *P. borealis* stocks in the ICES area and only one of the four in the NAFO area currently have precautionary-approach reference points (a limit mortality rate, Z_{MSY}, for West Greenland shrimp stock was proposed by the NAFO Scientific Council in November 2002; Hvingel and Kingsley 2002; NAFO 2002). Application of PA reference points for Pacific Pandalid stocks also appears to be lagging behind finfish applications.

Ironically, the precautionary approach, as implemented by PA reference points, is only being applied to resources with precise stock assessments, and the precautionary approach is not applied to resources with high uncertainty. This contradicts one of the precautionary-approach requirements summarized by Mace (1996): "The precautionary approach to fishery management is applicable even with very limited information". According to Garcia (1996*a*), management of highly uncertain systems should apply the precautionary principle, in which fisheries should be prohibited until there is evidence that catch is sustainable. Such advice is clearly not being practiced, and there appears to be a management void for most Pandalid stocks, which typically have uncertain assessments. Shrimp species with relatively short lifespans, late transition to mature females, and schooling behavior have high risk of recruitment overfishing and require management based on spawning stock biomass (SSB), recruitment or F reference points (Garcia 1996*b*). Therefore, the general lack of reference points for Pandalid shrimp stocks jeopardizes the long-term sustainability of shrimp fisheries.

Our objectives in this review are to explore the various approaches to deriving reference points for Pandalid shrimp and to evaluate their performance as candidates for targets or limits. Our review is structured in a hierarchical format from simple analyses that require less stock assessment information to highly complex models that require extensive research and monitoring programs. We will develop the argument that interim reference points and default precautionary targets should be used in uncertain situations. Furthermore, we advocate successive advances in reference point estimation and the required advances in research programs. Such a hierarchical approach to reference point estimation may provide a precautionary approach to managing Pandalid fisheries.

A hierarchy of reference point methods

Historical proxies

Many Pandalid shrimp stocks are assessed using survey or commercial catch rate information in which indices of stock biomass and recruitment are compared to historic observations that represent a desirable stock condition. Survey catches can be used to index relative stock size and demographics, including indices of total biomass, female biomass (i.e., SSB), or abundance of young shrimp (e.g., age-1 recruitment). Fishery catch rates are also commonly used to index exploitable biomass. In some cases, catch rates are standardized by species, area, season, vessel size, and gear (Boutillier et al. 1997; Hvingel et al. 2000; NAFO 2001). In

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some shrimp trap fisheries, catch rates by sex are standardized by trap type, length of soak, and area (Boutillier and Sloan 1988; Boutillier and Bond 2000). Relative exploitation rates can also be derived from either standardized effort or the ratio of observed catch to survey biomass (e.g., NAFO 2001).

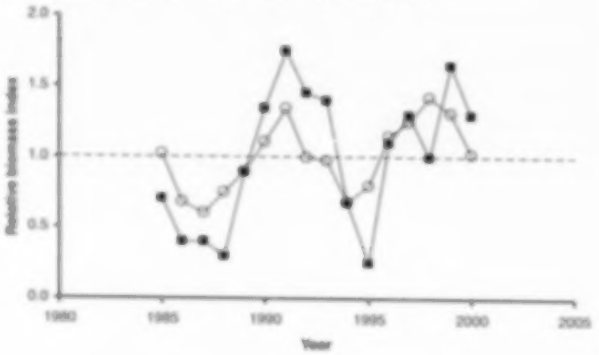
Stock status determinations are usually made by comparing current and past survey indices (e.g., ICES 2001; NAFO 2001; Orr et al. 2002). In some cases, conclusions that are usually based on PA reference points are based on comparisons to historical survey indices. For example, ICES (2001) concluded that the northeast Arctic shrimp stock was "probably within safe biological limits" because "surveys indicate that the biomass is close to the 1985–2000 average" (Fig. 1). Therefore, the 1985–2000 average biomass index is implicitly used as a target reference point. However, the same stock status determination was made in 2002 when both survey indices decreased to less than the historic average (ICES 2002). This illustration shows that forming an objective conclusion about stock status is difficult without explicit target and limit reference points (Hvingel 1997; Orensanz et al. 1998).

An example of the failure of descriptive reference points for managing sustainable harvests was the history of Kachemak Bay shrimp described by Fu et al. (2000). Annual "guideline" yield, a target catch determined from historic landings and survey biomass indices, was sequentially increased from 2000 t in 1977 to 2270 t in 1982. However, the fishery could not achieve the 1982 guideline yield. The survey biomass index substantially decreased in 1983. The fishery was closed and had not recovered as of 2000. Although the decrease in Kachemak Bay shrimp may have been influenced by cod predation or other environmental changes, the descriptive stock assessment did not detect the declining stock biomass during the early 1980s (Fu et al. 2000).

One recent trend in the assessment and management of Pandalid shrimp fisheries is the "traffic-light" approach, which considers a variety of information sources to determine stock status for the basis of management advice (Koeller et al. 2000*c*). The analogy to traffic lights is that each stock status measure is assigned a qualitative good or bad (green or red) signal and those signals will be used to determine stock status and to formulate management advice. Most applications include many signals, including anecdotal perceptions from fishermen and political and economic indicators. Koeller et al. (2000*c*) state that the advantages of the traffic-light approach are that it allows "intellectual and political equality to all stakeholders" and it is more precautionary than traditional stock assessment methods.

In an evaluation of precautionary reference points for Flemish Cap shrimp, NAFO considered the traffic-light approach and concluded that the approach was acceptable for providing a format for discussions among fishermen, scientists, and managers (NAFO 1999*a*, 1999*b*). However, they also concluded that the approach could only provide short-term perspectives on stock status and could not evaluate long-term management strategies. Furthermore, they felt that the approach cannot replace more conventional reference points and should only be used to supplement the traditional basis for management advice (NAFO 1999*a*). The NAFO Scientific Council currently uses the traffic-light approach as an interim measure for evaluating status of shrimp stocks (NAFO 1999*b*).

Fig. 1. An example of determining stock status by comparing current survey indices with historic observations. Biomass indices of northeast Arctic shrimp (*Pandalus borealis*) from Skagerrak and Norwegian (circles) and Russian (squares) surveys, scaled to the 1985–2000 mean (broken line; from ICES 2001).



Opinions vary on the role of the traffic-light approach in the management of Pandalid shrimp fisheries (see discussion from the Millennium Pandalid Shrimp Fisheries Symposium, Koeller et al. 2000*a*). Many shrimp biologists consider the approach to be a more reliable basis for stock status determinations than conventional reference points. We view the traffic-light approach as a valuable method for managing data-poor situations and for defining the research needed to elevate the assessment to the next tier of information and reliability. For example, Koeller et al. (2000*c*) used a population simulator to emulate population dynamics of the Scotian Shelf shrimp stock and evaluate the performance of the traffic-light approach for management of the stock. Such simulation requires the compilation of the most reliable biological and fishery data and thereby identifies the elements that are required for estimating more conventional reference points (e.g., demographic production models, described below).

Analytical stock assessments provide estimates of fishing mortality and absolute stock size, which can also be compared to empirically based reference points. A comprehensive review of methods for estimating F and stock size for crustacean populations is provided by Smith and Addison (2003). For example, the lowest observed stock biomass (B_{low}) has been proposed as a limit reference point for shrimp in the Skagerrak and Norwegian Deeps (ICES 2003). Limit and target F reference points were also proposed from a time series of F and biomass estimates for Gulf of Maine shrimp (Cadrin et al. 1999; Clark et al. 2000; Fig. 2, Table 1). The average F that preceded the stock collapse of the mid-1970s (0.7) was proposed as a limit reference point, and the average F during a period of apparent sustainability (average 1985–1995 $F = 0.34$) was proposed as an interim target. One technical problem with historical proxies is the comparability of historic estimates to current estimates. For the Gulf of Maine shrimp example, substantial changes in fishing gear and resulting size selectivity from the 1960s to the late 1990s made comparisons of F estimates among periods difficult. Therefore, the limit reference point for Gulf of Maine shrimp was more appropriately defined in percent of

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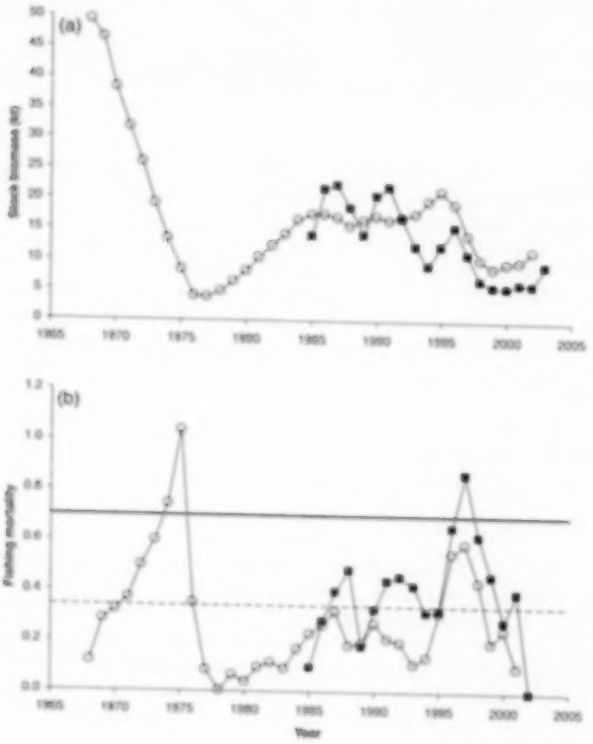
Fig. 2. An example of determining stock status by comparing current stock assessment results with historic estimates. Estimates of (*a*) stock biomass and (*b*) fishing mortality for Gulf of Maine shrimp (*Pandalus borealis*) from a biomass dynamics model (circles) and a Collie–Sissenwine analysis (squares) with the limit fishing mortality (1970s average, solid horizontal line) and the target fishing mortality (1985–1995 average, broken horizontal line).



maximum egg production per recruit (described below in Dynamic pool approaches).

A more objective approach to determining a sustainable exploitation rate is Rago's replacement ratio (NEFSC 2002). The method derives the relative exploitation rate that allows the population to replace itself using information from total catch and indices of relative stock size (e.g., survey data or fishery catch rates). The rate of change in the stock size index is derived as the ratio of stock size in a given year to the average stock size in previous years (e.g., for the lifespan of Gulf of Maine shrimp a 3-year average was considered to be appropriate). The log rate of change is regressed on the log exploitation ratio (catch-biomass index^{-1}). The relative exploitation rate that is expected to produce a rate of change equal to one is the replacement ratio. Given that relative exploitation rates greater than the replacement rate are not usually sustainable, the replacement rate should be considered as a limit reference point. Results for Gulf of Maine shrimp agree somewhat with the historical proxy described above, because the stock was not replacing itself (rate of change <1) in the mid-1970s when the relative exploitation rate was high but was quickly rebuilt when relative exploitation rates decreased in the late 1970s and early 1980s (rate of change >1) and was relatively stable (rate of change ~1) during the late 1980s and early 1990s (Fig. 3). However, the estimated replacement rate is somewhat sensitive to the observed rate of change in 1978 when the fishery was closed; a regression with that observation removed estimated a much greater replacement rate.

A limitation of historical proxies is their short-term perspective relative to periods before the fishery developed and their general tendency toward underestimating stock productivity (Greene 2002). For the Gulf of Maine shrimp example, the target F sustained moderate stock biomass in the past, but a lower target may produce greater long-term yield. Furthermore, using recent averages as proxy reference points may creep toward greater fishing mortality or lower stock biomass as stocks decline. Therefore, without the requisite modeling of population dynamics, such empirical proxies may be limited by the observed dynamic range of the stock, may not be sustainable, or may not represent conditions for optimal productivity.

Biomass dynamics approaches

The simplest theoretical approach to estimating reference points is based on biomass dynamics in which an informative history of catch and relative stock size or fishing effort can be used to determine stock status relative to MSY reference points. The most common production function used to model biomass dynamics is the logistic growth model:

$$(1) \qquad \frac{\partial B}{\partial t} = rB_t - \frac{r}{K}B_t^2$$

in which the change in stock biomass over time is a quadratic function of biomass (B), r is the instantaneous annual growth rate, and K is the carrying capacity. Schaefer (1957) added a yield term to model a fished stock, so that the rate of change is reduced by yield (Y, in units of biomass):

$$(2) \qquad \frac{\partial B}{\partial t} = rB_t - \frac{r}{K}B_t^2 - Y_t$$

The production parameters r and K can be used to derive MSY reference points directly:

$$(3) \qquad \mathrm{MSY} = \frac{rk}{4}$$

$$(4) \qquad B_{\mathrm{MSY}} = \frac{K}{2}$$

$$(5) \qquad F_{\mathrm{MSY}} = \frac{r}{2}$$

As described by Mace (2001), F_{MSY} should be applied as a limit reference point. Pella and Tomlinson (1969) generalized the Schaefer model to allow for alternatives to logistic growth assumptions:

$$(6) \qquad \frac{\partial B}{\partial t} = rB_t - \frac{r}{K}B_t^m - Y_t$$

where m is a shape parameter for the production function. If $m = 2$, eqs. 1 and 6 are equal and growth is logistic. As m approaches 1, Gompertz growth is assumed, as in the Fox (1970) model. The shape parameter, m, also has influence on MSY reference points:

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Table 1. Estimates of biological reference points for Gulf of Maine shrimp from various methods.

Reference point	Estimate[a]	Method	Reference	Current application
$F_{1985\text{–}1995}$	0.34	Historical proxy	Cadrin et al. 1999	Target
F_{1970s}	0.70	Historical proxy	Cadrin et al. 1999	Limit
F_{MSY}	0.17	Biomass dynamics	NEFSC 2003	None
B_{MSY}	30 000 t	Biomass dynamics	NEFSC 2003	None
F_{max}	1.0–1.5	Yield-per-recruit	Clark 1981, 1982	None
$F_{40\%}$	0.77	Yield-per-recruit	Cadrin et al. 1999	None
$F_{0.1}$	0.46	Yield-per-recruit	Cadrin et al. 1999	None
$F_{30\%}$	0.25	Eggs-per-recruit	Cadrin et al. 1999	Rebuilding target

[a] F reference points are for fully recruited sizes and ages, except for F_{MSY} from the biomass dynamics model which is on all ages, weighted by biomass.

$$\text{(7)} \qquad \text{MSY} = r\left(1-\frac{1}{m}\right)\cdot\left(\frac{K}{m}\right)^{\frac{1}{(m-1)}}$$

$$\text{(8)} \qquad B_{\text{MSY}} = \left(\frac{K}{m}\right)^{\frac{1}{(m-1)}}$$

$$\text{(9)} \qquad F_{\text{MSY}} = r\left(1-\frac{1}{m}\right)$$

Biomass dynamics models have been applied to several Pandalid fisheries. For example, Abramson and Tomlinson (1972) estimated that F_{MSY} of Californian ocean shrimp was 0.5 using a Schaefer model. Skúladóttir (1979, 1981) estimated MSY reference points for Icelandic shrimp by regressing fishery catch rates on effort (Fig. 4) and by regressing yield on catch rates assuming logistic growth. Alternatively, a Fox model was also assumed for yield on catch rate regressions, but estimates of r and MSY were similar between model choices (Skúladóttir 1979). Skúladóttir (1985, 1990) also modeled the exponential relationship of yield on fishery catch rates to estimate MSY reference points for Denmark Strait shrimp.

Methods for biomass dynamics modeling have advanced considerably in the last decade. Time-series estimators are considered to be more reliable than traditional linearization methods (Hilborn and Walters 1992; Polachek et al. 1993). Advanced applications include bootstrapped variance estimates. For example, ASPIC (a stock production model incorporating covariates, Prager 1994) was used to estimate the status of Denmark Strait shrimp relative to MSY reference points and to project stock size for alternative management decisions (Cadrin and Skúladóttir 1998; Fig. 5). Variance estimates can also be derived using the jackknife method, as demonstrated by Hvingel and Kingsley (2000) for West Greenland shrimp, or posterior probabilities (Hvingel and Kingsley 2001, 2002). Variance of F_{MSY} estimates is useful for deriving precautionary targets (Prager et al. 2003)

Another advantage of the ASPIC program is the potential for using multiple indices of stock biomass. For example, three survey series were used to model biomass dynamics of Gulf of Maine shrimp (Cadrin et al. 1999; Clark et al. 2000), and simulation analyses indicated that trends in stock biomass were accurate when catch and relative stock size indices were measured with moderate to high precision (Cadrin 2000). Simulations by Prager et al. (1996) also suggest that relative trends, expressed as B_t/B_{MSY} and F_t/F_{MSY} may be more reliable that absolute estimates of biomass or F from ASPIC. In comparison to the reference points based on historical proxies for Gulf of Maine shrimp, described above, the ASPIC estimate of F_{MSY} for Gulf of Maine shrimp (0.17; NEFSC 2003) is much less than the target based on historical proxies (0.34), and the B_{MSY} estimate (30 000 t) is greater than the stock size estimates during the chosen period of sustainability (approximately 17 000 t during 1985–1995, Table 1).

Surplus production (SP) can also be calculated from any stock assessment that provides estimates of catch and biomass (Jacobson et al. 2002):

$$\text{(10)} \qquad \text{SP}_t = B_{t+1} - B_t + \delta Y_t$$

where δ is a coefficient that accounts for timing of the catch and production of fish caught so that $B_{t+1} + \delta Y_t$ is the biomass that would have been produced with no catch (MacCall 1978). Given an informative series of observations, (i.e., one with a wide dynamic range), surplus production can be used to estimate the production parameters in eqs. 1 or 6, because it is a discrete observation of change in biomass over time ($\partial B/\partial t$).

An advantage of biomass dynamics models is the power of simplicity. The tractable nature of the model facilitates the testing of other important model components. Biomass dynamics models for Pandalid shrimp can be modified by the addition of a predation term. The Schaeffer model (eq. 2) and the more generalized model (eq. 6) can be viewed as predator models, because a single-species model (i.e., eq. 1) was extended by adding a term for removal by another species (i.e., the fishery, in eq. 2). The "single-predator" model can easily be expanded to a two-predator model by adding another predation term:

$$\text{(11)} \qquad \frac{\partial B}{\partial t} = rB_t - \frac{r}{K}B_t^m - Y_t - cP_t$$

where c is the predation rate and P_t is the biomass of the predator population. From a model-building perspective, the significance of parameters r, K, and c in explaining variance in biomass dynamics can be tested using multiple linear regression of annual surplus production (Ricker 1975) or nonlinear regression through time-series analysis (Hilborn and Walters 1992).

For example, Stefánsson et al. (1994) added a term for cod predation on Icelandic shrimp because the biomass of

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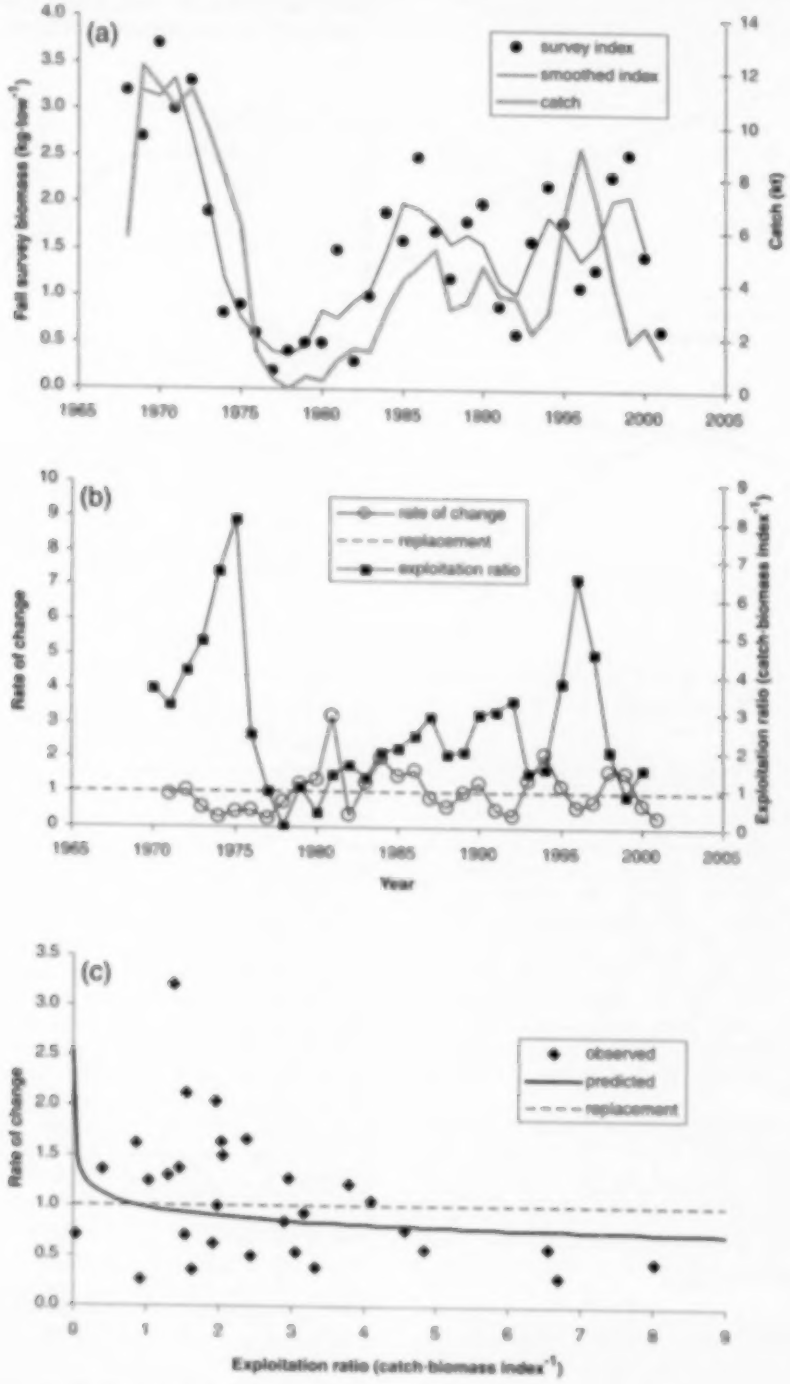
Fig. 3. Application of Rago's replacement ratio method to Gulf of Maine shrimp (*Pandalus borealis*), in which (*a*) catch and indices of stock biomass are used to derive (*b*) the rate of change and exploitation ratio and (*c*) are regressed to estimate the exploitation rate that allows replacement.



cod has a great influence on the growth rate of the shrimp population. The model is also used to assess shrimp in the Skagerrak and Norwegian Deeps (ICES 2003). However, the production model developed by Stefánsson et al. (1994) cannot be used to derive MSY reference points because it does not include the density dependence term *K*. Density depend-

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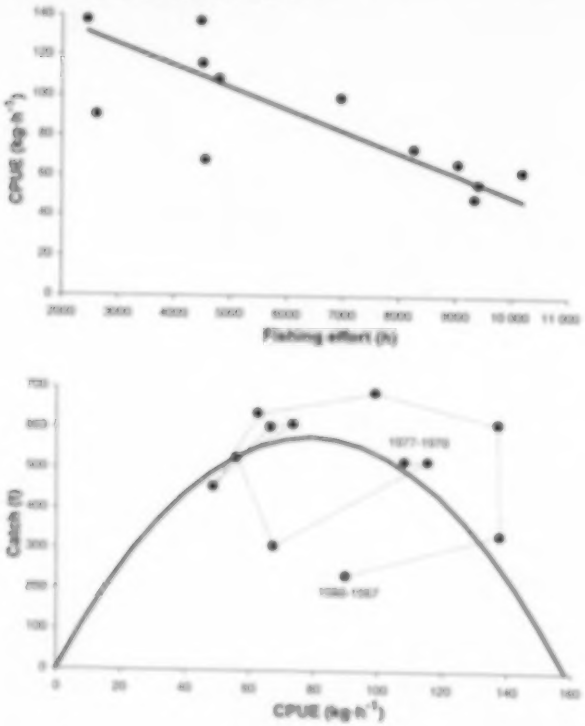
Fig. 4. Biomass dynamics of Icelandic shrimp (*Pandalus borealis*; observations, circles; predicted, lines; data are from Skúladottir 1981). CPUE, catch per unit effort.



ence was included in a production model with predation by Hvingel and Kingsley (2001), who used a Bayesian analysis to investigate the effects of cod predation on the biomass dynamics of West Greenland shrimp. However, the predation term, which is structured as a type III functional response (Holling 1959), did not improve the goodness of fit to the data. A revised analysis also indicated that the predation model had only slightly better fit to the data, but MSY reference points were estimated with much greater precision (Hvingel and Kingsley 2002; Fig. 6). Information on predator biomass may be available from stock assessments, but the geographic overlap between predators and shrimp stocks, as well as the annual variation in distributions, should be considered.

Abiotic factors that influence biomass dynamics can also be incorporated into production models. For example, temperature has a substantial effect on the dynamics of many shrimp populations and can be expressed as an additional term in the production model:

$$(12) \qquad \frac{\partial B}{\partial t} = rB_t - \frac{r}{K}B_t^m - Y_t + gT_t$$

where g is the temperature effect on population growth (the sign of the coefficient indicating a positive or negative influence), and T_t is annual mean temperature. If temperature is expressed as an anomaly (i.e., the time series has a mean of zero), then MSY reference points for average temperature conditions can be derived using eqs. 3 to 5 for logistic growth (or eqs. 7 to 9 for the generalized form).

Fig. 5. Estimated stock biomass of Denmark Strait shrimp (*Pandalus borealis*) relative to B_{MSY} 1977–1999 and projected 2000 biomass assuming 5000 t catch in 1999 (modified from Cadrin and Skúladottir 1998). Dotted lines indicate 80% confidence limits, and the broken line indicates B_{MSY}.

For example, several studies have concluded that landings of shrimp in the Gulf of Maine are correlated to temperature (reviewed in Clark et al. 2000). The influence of temperature on biomass dynamics of Gulf of Maine shrimp was tested using a nonlinear regression in which model improvement was evaluated as an F ratio (Prager 1994):

$$(13) \qquad F = \frac{(\mathrm{RSS}_2 - \mathrm{RSS}_{12})}{\left(\frac{\mathrm{RSS}_{12}}{\mathrm{df}}\right)}$$

where RSS is residual sum of squares, df is the degrees of freedom (observations minus parameters), and subscripts indicate models in eq. 2 and eq. 12. The addition of a term for spring surface temperature anomaly in the western Gulf of Maine (the variable most often associated with shrimp productivity; Richards et al. 1996; Clark et al. 2000) did not appreciably improve the fit of the model to the data ($g \approx 0$, $F \approx 0$ for time lags of 0 to 3 years).

The major disadvantage of biomass dynamics models is the lack of information on demographic stock structure. Aggregate indices of stock biomass and total yield are not sensitive to transient conditions (e.g., recruitment episodes), and stock status relative to MSY reference points, as determined by biomass dynamics models, may be misleading. For example, production models assume that the per capita growth rate is greatest at extremely low stock sizes (i.e., compensatory growth), but depleted stocks typically have severely truncated age structure and low reproductive potential (i.e., depensatory growth). The Stefánsson et al. (1994) model, mentioned above, includes a recruitment term rather than relying on an aggregate growth rate:

$$(14) \qquad B_{t+1} = aB_t + R_t - Y_t - cP_t$$

where a is growth in biomass and R is annual recruitment.

Although the data requirements for biomass dynamics modeling are few (aggregate catch and biomass indices), several periods of depletion and rebuilding over a wide dynamic range are necessary for reliable estimates of MSY reference points (Hilborn and Walters 1992). Applications of biomass dynamics models to Pandalid shrimp populations demonstrate the utility of the approach for estimating refer-

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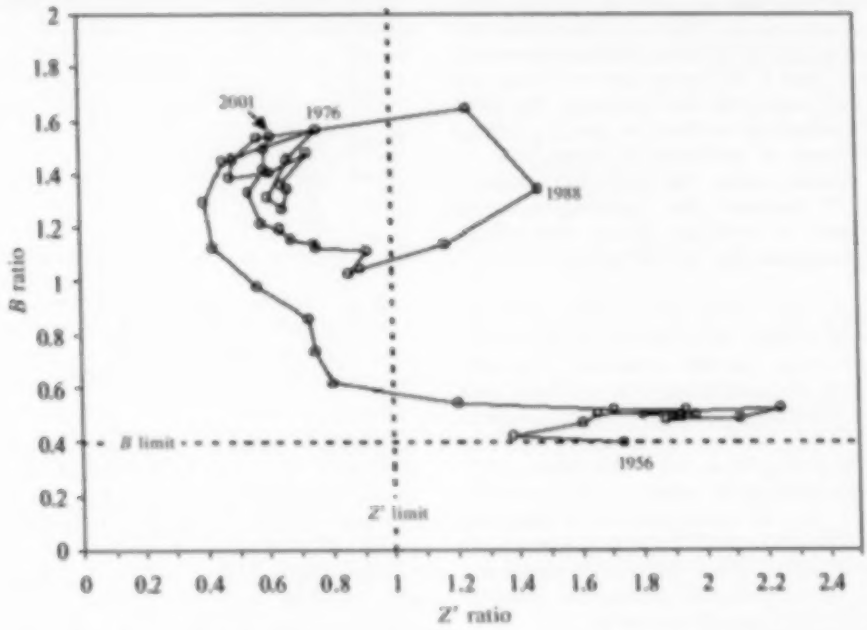
Fig. 6. Estimated annual median biomass ratio (B/B_{MSY}) and mortality ratio (Z/Z_{MSY}) from a production model of West Greenland shrimp (*Pandalus borealis*) with cod (*Gadus morhua*) predation, 1956–2002 with proposed limit reference points (from Hvingel and Kingsley 2002).



ence points and the potential for testing future directions for research (e.g., quantifying the effect of predators or environmental factors). Therefore, biomass dynamics models should be considered as a valuable step in the hierarchy of methods, between historical proxies and more informative methods.

Dynamic pool approaches

Dynamic pool analysis can be designed using life history and fishery information to produce estimates of yield per recruit (YPR), spawning biomass per recruit (SPR), and percent maximum spawning potential (%MSP) reference points, either in an "age-based" format (Thompson and Bell 1934; Ricker 1954) that accounts for protandry or a length-based format (e.g., Beverton and Holt 1957). Furthermore, dynamic pool models can incorporate nontraditional discrete growth with transitions through complex life history stages (e.g., Shepherd and Idoine 1993). The SPR approach was developed for dioecious life histories in which proportion mature at age is used to calculate spawning biomass, but proportion female at age can be used to model protandry, providing female biomass per recruit or eggs per recruit as an index of spawning potential.

There are several examples of applying traditional age-based YPR analysis to Pandalid shrimp. Skúladóttir (1979) calculated YPR for Icelandic shrimp using the Thompson and Bell (1934) age-based method, with F at age from cohort analysis, observed mean weights at age, and assuming a range of natural mortality (M) from 0.2 to 0.4. She found that F_{max} (the F that produces maximum YPR) was approximately 0.4 when M was assumed to be 0.2, but F_{max} was not well defined for greater M assumptions. The reference point F_{max} is often used as a proxy for F_{MSY}, implicitly assuming that recruitment is independent of stock size, and can therefore be considered as a limit reference point in some situations. The fishing mortality associated with one-tenth of the initial increase in YPR from $F = 0$, termed $F_{0.1}$, is a target reference point intended to produce nearly maximum YPR while maintaining greater stock size. Clark (1981, 1982) calculated YPR for Gulf of Maine shrimp using Ricker's (1975) method using mesh-selection curves and assuming a range of M from 0.25 to 1.0, increasing with age. Estimates of F_{max} varied from 1.0 to 1.5 (Clark 1981, 1982).

Yield per recruit and percent maximum spawning potential (Gabriel et al. 1989; Goodyear 1993) were estimated for the Gulf of Maine northern shrimp fishery (Cadrin et al. 1999; Clark et al. 2000). Length at age was estimated using von Bertalanffy growth parameters, selectivity at size was estimated using a selectivity curve, and mean weight at length for males and females was estimated using published relationships. Batch fecundity was estimated by a linear relationship to carapace length, proportion female at the time of hatch was estimated by observed sex ratios at length, and M was assumed to be 0.25. Results indicated that F_{max} was 0.77, and the increase in yield per unit F decreased to one-tenth of the initial increase at $F = 0.46$ ($F_{0.1}$). Spawning potential was reduced to one-half of the maximum spawning potential (measured as egg production per recruit) at $F = 0.25$ ($F_{30\%}$; Fig. 7).

Results from an age-based assessment of Norwegian Deeps and Skagerrak shrimp were used to estimate YPR and SPR reference points (ICES 2000). In comparison to Gulf of Maine shrimp, the assumed M was much greater (0.75), and resulting reference point estimates were also greater (e.g., $F_{0.1} = 0.76$, $F_{35\%} = 0.90$).

Anthony (1982) offers the rule of thumb that dynamic pool models should be simulated to a maximum age at which

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5% of the initial cohort abundance survives with no fishing (this rule of thumb can also be expressed as maximum age = $3/M$; Gabriel et al. 1989). Based on a disparity between published estimates of lifespan and the estimate of M for Gulf of Maine shrimp, Cadrin et al. (1999) simulated yield and egg production through age-7, but also considered two alternative analyses, one used a maximum ages of 12 and the other simulated an increase in M after spawning. The alternative analysis that simulated survival to age-12 produced slightly greater estimates of maximum YPR and MSP, as well as lower F reference points. The exploratory analysis that assumed that M increased after spawning produced slightly lower estimates of yield per recruit, substantially lower estimates of maximum eggs per recruit, and greater F reference points.

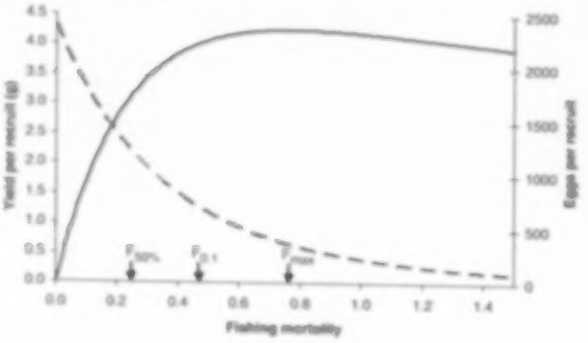
Traditional dynamic pool approaches calculate yield and spawning potential of a cohort as a summation across discrete age increments, under specified conditions of growth, vulnerability to fishing, and natural mortalities. Within each age interval, growth and fishing mortality rates are assumed to apply uniformly to all members of the cohort (Gulland 1977). However, not all individuals follow the same growth trajectory, and the susceptibility of individuals to mortality is often at size rather than an age-dependent phenomenon (Kirkpatrick 1984). Consequently, length-based models can provide a more precise and accurate depiction of cohort dynamics, in addition to using directly measurable variables that are often linked to management measures.

Age-based dynamic pool models may be particularly inappropriate for species with unusual or complex life histories, such as Pandalid shrimp (Perry et al. 1999). This may be true for hermaphroditic species that have unique reproductive stages that change as a function of size. For example, significant growth and mortality changes that occur following sexual transformation may not be adequately accounted for in conventional dynamic pool models (Shepherd and Idoine 1993).

Another aspect of modeling Pandalid shrimp life history is the mechanism of growth. In terms of length, crustaceans grow discontinuously (Hartnoll 1982). The frequency of the molting process and the difference in the size of the old and new shell determine the growth rate of a shrimp. Because these processes interact and are variable with size, it is difficult to explicitly determine a representative rate with a measure of variation. Therefore, size-specific models that combine the effects of variable duration at size (molt frequency) and molt increment are well suited for describing growth for crustaceans (Idoine and Finn 1984; Fogarty and Idoine 1988). The addition of stage-specific rates and transition between these states allow the development of a growth – life history model that can accommodate the complexity of Pandalid shrimp. Simulations can reflect average environmental conditions or environmental effects, which can be included in the model as control variables.

Discontinuous growth can be modeled as a series of residence times spent at successive sizes within life history stages. For example, growth in Gulf of Maine shrimp is sexually dimorphic and has three possible growth rates: female, immature male, and transitional. One approach for modeling growth is the use of delay models. Delay models were first

Fig. 7. Yield and egg production per recruit of Gulf of Maine shrimp (*Pandalus borealis*) as a function of fishing mortality and associated reference points (solid line indicates yield per recruit, and the broken line indicates eggs per recruit; modified from Cadrin et al. 1999).



developed in the field of industrial dynamics as a technique to monitor movement of individuals through a system of substages (Forrester 1961) and have since been modified to incorporate effects of attrition (mortality) and variability in timing of movements (Manetsch 1976; Vansickle 1977). Similar to environmental effects on growth, predation can be included in the model as a control variable. The subclass of distributed delay models can be a useful tool to describe the movement of any item through a process or, in a biological context, through developmental stages (Manetsch 1976). Extended models that include a series of consecutive processes have been used to simulate growth dynamics in marine crustaceans (Idoine and Finn 1984) and hermaphroditic finfish (Shepherd and Idoine 1993). The major advantage of this model type is its focus on the aggregated behavior of individuals rather than a representative mean. With this approach, one can model growth as a series of distributed delays with an associated mortality, using length categories as individual developmental stages. This approach retains information about variation in size composition and size-specific mortality during the simulated decline of a cohort (or multiple cohorts).

The structure of distributed delay models can be characterized as a sequence of stages, with flow through each stage. For example, the life history of Gulf of Maine shrimp can be viewed as a series of life history stages (larval, immature, male, transitional, and female; Fig. 8), as described in Fox (1973) for a similar Pandalid population. The model can be simulated as a series of difference equations with a time step equal to 1 day. Within each state, there are subdivisions representing length groups at appropriate intervals (e.g., 0.1-mm carapace length, CL). The delay model can be expressed in terms of either flows or state variables. For simulation purposes, the model utilizes flows within, between, and out of stages that represent length categories through which shrimp will pass. Flows can be converted to state variables (e.g., numbers of individuals dead due to fishing mortality at a given size) where necessary for analyses. Individuals in the cohort passed through each stage at a rate determined by a probability density function. Transit time of

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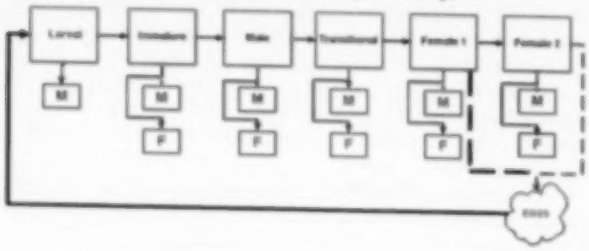
Fig. 8. Life history diagram for Gulf of Maine shrimp, *Pandalus borealis* (M, natural mortality; F, fishing mortality).



an individual through a stage is a function of the mean delay period and associated variance.

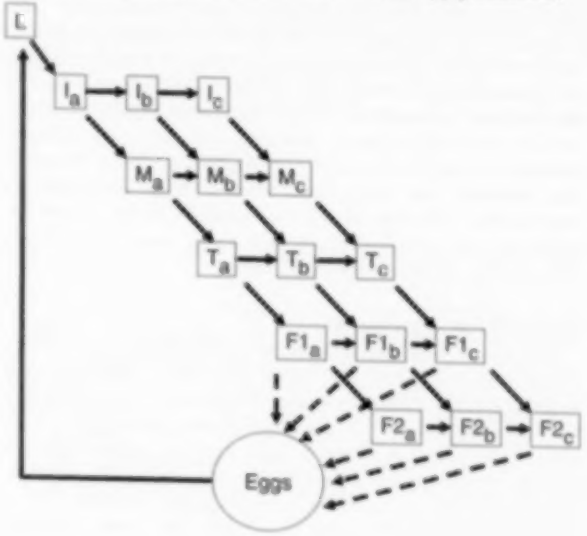
When crustaceans molt, the increase in shell size is often a range of sizes of molt intervals, mi (e.g., Fogarty and Idoine 1988). At time $t + 1$, shrimp either move into length stage $i +$ mi, remain in length stage i (at some substage), or are removed from the system at a defined rate of mortality due to sex- and size-specific fishing and (or) natural mortality. At time $t + 2$, some shrimp are still in stage i, some in $i + 1$, and possibly some in $i + 2$, etc. Biomass and mean size change as the distribution moves through the series of length stages. Yield can be calculated from the number of individuals at size removed by fishing. Additionally, a function to examine effects of discarding can be included. The number of mature females at length can be converted to biomass using a length–weight equation. In a similar fashion, egg production can be estimated by applying size-specific fecundity to the spawning stock.

Hermaphroditism is modeled by separating the population into sex-based states and using a size-specific probability of sex transformation from male to female. Over a designated length interval, males transform by passing through an intermediate transitional stage before entering the female growth sequence (Fig. 9). With this structure, one may examine a wide array of population responses to external (e.g., fishing, temperature, or predation) perturbations.

The following are input parameters required for the model: mean transit time, and its associated variance, per appropriate length category (e.g., 0.1-mm CL) by stage; range of lengths for each sex in the population; range of molt increments (specific to length groups and sex if appropriate); probability of sex transformation at length; range of lengths at recruitment (L_c, critical length) to the fishery; instantaneous natural mortality rate (specific to length groups and sex if appropriate); and the percentage of females mature at length. Length–weight equations by sex are necessary for conversion of numbers at length to biomass, and fecundity at length is required for egg production calculations. The need for representative values by each size, stage, and, in some instances, time of year (day) is beyond our current knowledge for most Pandalid shrimp stocks.

As discussed in the demographic production model section below, the full life history model can also be simulated as a population of cohorts linked by the hatched eggs that result in larvae (Fig. 9). The cohort representation can be used to examine reference points appropriate to those aspects of the population at equilibrium. A range of harvesting strategies can be examined to estimate an expected response to

Fig. 9. Schematic description of flow between life history stages (sex-specific length intervals) for Gulf of Maine shrimp, *Pandalus borealis* (L, larvae; I, immature; M, mature males; T, transitional between males and female; F1, 1st-year females; F2, 2nd-year females; Eggs, eggs that successfully hatch; a, b, and c indicate size groups, and broken lines indicate egg production).



long-term average conditions. Because these are per-recruit analyses, another way of viewing this is how to utilize a given cohort. These approaches can include variations on selectivity at length patterns, seasonal limitations on harvesting, and rates of discarding and discard mortality.

Unfortunately, the appropriate %MSP for determining target and limit reference points is somewhat arbitrary. However, %MSP may have advantages over F for comparing fishery development from different periods. For example, the stock collapse in the 1970s may provide guidance on the level of sustainable F for Gulf of Maine northern shrimp. However, size selectivity during the 1970s was much different than that simulated for yield and egg production per recruit from the current fishery. Accordingly, an additional analysis was conducted assuming a historical estimate of selectivity to approximate historical levels of egg production. Based on estimates of F from ASPIC and survey length frequencies (Clark and Anthony 1981), as well as the egg per recruit analysis that assumed historical selectivity, spawning potential was reduced to less than 10% of maximum. Therefore, $F_{10\%}$ may be a candidate for a limit reference point. Conversely, the Gulf of Maine shrimp stock was relatively stable when SPR was approximately 40% of maximum (Cadrin et al. 1999), and $F_{40\%}$ could be a target.

One limitation of dynamic pool approaches is that developmental rates may be variable and density-dependant. For example, protandrous transition can be accelerated at low stock size and delayed for extremely abundant cohorts (e.g., Koeller et al. 2000*b*). The implications of compensatory maturation are that dynamic pool methods may underestimate egg production at low abundance (i.e., high F) and overestimate egg production at high abundance (i.e., low F).

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However, assuming a constant maturity schedule is more risk averse than incorporating density-dependent compensation.

Another drawback of dynamic pool approaches for determining reference points is the implicit assumption of stationary recruitment. Regardless of the level of F and the resulting %MSP, a steady stream of recruitment is assumed to continue. Such an assumption is risk prone if recruitment fails at low stock sizes. Furthermore, YPR analyses usually suggest an optimal fishery selectivity that involved high retention of small males, but such selection is not economically efficient, and low survival to female maturity will risk stock collapse (Abramson and Tomlinson 1972; Anderson 1991). Nonetheless, dynamic pool approaches offer a viable alternative to determining reference points for Pandalid shrimp when information on growth, fishery selectivity, natural mortality, and maturity or fecundity is available.

Stock–recruit approaches

The use of stock–recruit relationships in setting of reference points is reviewed by Gabriel and Mace (1999) in terms of the types of features in a spawner–recruit relationship that serve as reference points in semelparous populations. This type of analysis is not readily used in most shrimp fisheries because stock–recruit relationships can rarely be demonstrated (Koeller et al. 2000c). Hilborn and Walters (1992) state that stock–recruit relationships are "the most important and generally the most difficult problem in fisheries science". The difficulty arises in that the relationship is confounded by a number of factors such as our ability to define a population and understand the relationship to a larger metapopulation and our ability to distinguish between the spawner–recruit relationship and the other abiotic and biotic factors influencing recruitment. Myers and Barrowman (1996) point out in their meta-analysis of 364 fish stocks, "recruitment over-fishing appears to be a common problem" and "fish populations should be managed to maintain sufficient spawner abundance to yield high recruitment".

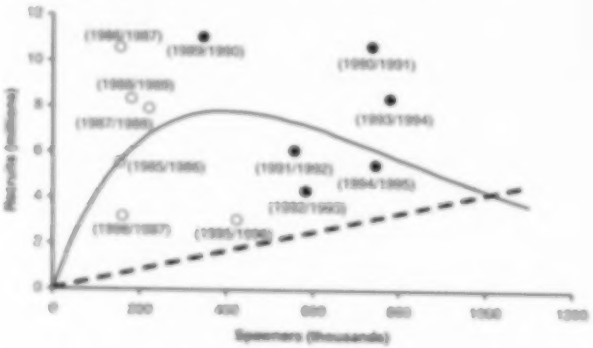
Hilborn and Walters (1992) define three approaches to describe stock–recruitment relationships: "rough and ready", stock–recruitment curves and variances, and tabular or Markov models. Examples of "rough and ready" reference points derived from stock–recruit patterns are F_{med}, the F that produces the SPR needed to replace the median observed recruit per spawner, F_{hi}, the F associated with replacing the 90th percentile of recruit per spawner, and F_{lo}, the F associated with replacing the 10th percentile of recruit per spawner. Management of the Norwegian Deeps and Skagerrak shrimp has been based on F_{med}, where it was estimated to be 0.65 (F_{hi} = 1.83, F_{lo} = 0.23; ICES 2000), though subsequent assessments found the age-based analysis and stock–recruit estimates to be suspect (ICES 2001).

The next tier of stock–recruit analysis involves fitting a theoretical function to spawners (S) and recruit (R) observations. A common relationship fit is the Ricker (1954) model:

$$(15) \quad R = \alpha S e^{-\beta S}$$

where α and β are estimated using nonlinear regression. Alternatively, stock–recruit parameters can be estimated using delay-difference models (Deriso 1980; Schnute 1985) involving an analysis of catch and stock size indices or age-based data.

Fig. 10. Ricker spawner–recruit relationships for prawns in the Howe Sound experimental management area using estimated number of spawners from cohort analysis (open and solid circles indicate observations from open and closed seasons, respectively, with labels indicating season of spawn; solid line is fitted curve, and broken line is replacement at $F = 0$; from Boutillier and Bond 2000).



Abramson and Tomlinson (1972) applied a Ricker model (eq. 15) to California ocean shrimp, but observations did not fit the model well. A Ricker stock–recruit model was also fit to Pavlof Bay shrimp using a survey index of females as a measure of spawning stock and a survey index of males as a measure of recruitment (Anderson 1991). Most observations fit the relationship well, with the exception of two extremely abundant year classes. Anderson (1991) concluded that YPR reference points were more appropriate because recruitment is greatly influenced by environmental factors.

Stock–recruit relationships were also used to set minimum monthly CPUE indices for females (a spawner escapement index) that form the basis for management of the *P. platyceros* trap fishery in British Columbia (Boutillier and Bond 2000). The history of the development of a referential decision system for *P. platyceros* follows, to a certain extent, the iterative approach to development of reference points mentioned previously. The initial reference points were established using a "rough and ready" analysis of catch and survey data from one area of the coast which was then applied to the whole coast. Experimental areas were then established along the coast to monitor population responses to a wide range of fishing pressures and population sizes. Modifications to the spawner index have since been recommended as a result of analysis using stock–recruitment curves and Markov models of these experimental area data sets, which have a fourfold variation in stock and recruitment (Fig. 10; Boutillier and Bond 2000). The data suggest increased recruitment as stock size increased from low abundance and decreased recruits per spawner at high stock size, with a lag to the density dependence (Fig. 10). In this case, the results of both types of analysis suggested that the original biomass reference points from "rough and ready" analysis were not conservative enough and the spawner escapement indices needed to be higher.

Hilborn and Walters (1992) conclude that the largest problem in addressing the issue around stock–recruitment is ob-

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taining proper estimates of spawners and recruits. Ludwig and Walters (1981) preformed simulations with explicit errors in measurement of spawning stocks and showed that even reasonably small random errors in measurement can change a true linear stock–recruitment relationship into something that shows little or no relationship. This does not mean that data quality is the only factor making stock–recruitment relationships difficult to understand. As we can see from the discussion on the biology of these animals, there are numerous confounding abiotic factors (e.g., temperature, wind direction) and biotic factors (e.g., predator abundance, cannibalism) that make the stock–recruitment process a complex stochastic phenomenon.

The Ricker function (eq. 15) can be extended to include abiotic factors:

$$R = \alpha S e^{-\beta S + \gamma T}$$

where γ is the effect of temperature (T) on recruitment. For example, Richards et al. (1996) found that the addition of a temperature term in the stock–recruit model explained 43% of variance in recruitment of shrimp in the Gulf of Maine. If annual temperature is expressed as an anomaly from the time series mean, resulting stock–recruit parameters can be used to derive reference points that are based on average temperature conditions.

Some of the key biological and fishery characteristics that British Columbia's *P. platyceros* trap fishery exhibits that helped contribute to the development of a spawner escape referential management system based on a stock–recruitment relationship are as follows. (*i*) Small isolated populations located in sheltered inshore inlets provide for better definition of a population and easier, more reliable assessments. (*ii*) The animals are semelparous so there is no need to complicate the analysis by having to incorporate different egg production for different ages and sizes of animals. (*iii*) The larvae are well developed and go through relatively few larval stages, which has implication on the extent of larval drift. (*iv*) These animals are benthic organisms and migration of adult animals is very restricted, as opposed to those shrimp that undergo diel vertical migrations or are pelagic and subjected to further dispersion with water movements. (*v*) These are large animals and data are easily collected in terms of numbers of animals without the need to subsample for counts and weights to estimate numbers. (*vi*) Animals do not exhibit primary females; therefore, the estimation of spawners is not confounded by compensatory biological mechanism. (*vii*) Information is readily collected on the target species, and other species of shrimp do not confound the assessment process.

Demographic production models

The top tier of reference point approaches merges dynamic pool and stock–recruit information to estimate production curves and MSY reference points. In its most basic form, a constant level of recruitment is multiplied by YPR and SPR at various levels of F to derive production curves that are simply scaled YPR and SPR curves. For example, Skúladóttir (1979) estimated equilibrium yield expectations for Icelandic shrimp as a product of average recruitment from cohort analysis and yield per recruit. The implicit assumption is similar to that of dynamic pool approaches — that recruitment is constant at all levels of F and all stock sizes and may not be valid for many Pandalid stocks.

Ideally, stock–recruitment relationships can be used to impose negative feedback, in the form of reduced recruitment at low stock size, resulting from high F (e.g., Beverton and Holt 1957; Sissenwine and Shepherd 1987). For iteroparous species, equilibrium recruitment (R_F^*) at a given F can be derived by replacing S in any stock–recruit function with ($R_F^* \cdot \mathrm{SPR}_F$) where SPR_F is the SSB per recruit at the given F. For example, equilibrium recruitment from a Ricker function (eq. 15) is

$$(17) \quad R_F^* = \frac{\ln(\alpha \mathrm{SPR}_F)}{\beta \mathrm{SPR}_F}$$

A yield curve can be derived as the product of R_F^* and YPR_F for a range of F values. An estimate of F_{MSY} can be derived as the F that produces the maximum equilibrium recruitment. For example, the stock and recruitment estimates for Norwegian Deeps and Skagerrak shrimp in combination with yield and spawner per recruit information (ICES 2001) can be used to develop a demographic production model. This example should be considered as illustrative only because of the uncertainty associated with age determination by cohort slicing, potential predator effects, and substantially greater biomass estimates from biomass dynamics models (ICES 2000, 2001). Based on a Ricker stock–recruit function, the expected production relationships correspond to the recently observed patterns of yield, biomass, and F (Fig. 11). However, estimates from such age-based production models are sensitive to stock–recruit predictions, assumed partial recruitment, and maturity schedules (e.g., Mohn and Black 1998; NEFSC 2001). For example, if yield and spawning biomass per recruit are derived from the reported mean weights at age, partial recruitment, and maturity schedule from the 2000 assessment of Norwegian Deeps and Skagerrak shrimp (ICES 2000) rather than the 2001 assessment (above), the estimate of MSY is substantially greater and well beyond the observed catch. Therefore, precise estimates of age-based parameters are essential for reliable estimates of MSY reference points from age-based production models.

Demographic production models are essentially population simulators that include the entire life cycle, projecting long-term yield and stock size at various levels of F. By comparison, dynamic pool models are population simulators with an incomplete life cycle, from recruitment to death. Accordingly, any population simulator can be used to evaluate candidate reference points (ICES 1997). For example, Fox (1973) used a simulation model with discontinuous growth, protandry, and a Beverton–Holt stock–recruit relationship to model equilibrium yield for a Pandalid shrimp population. He estimated MSY (5.5 billion shrimp) and F_{MSY} (1.0) based on equilibrium yield expectations.

Simulations can be used to explore alternative modeling assumptions. As an alternative to determining F_{MSY} from equilibrium expectations (above), F_{MSY} can be determined as the F that produces the maximum median yield from a distribution of expected yields from long-term stochastic simulation (Mace 2001). Koeller et al. (2000*c*) used simula-

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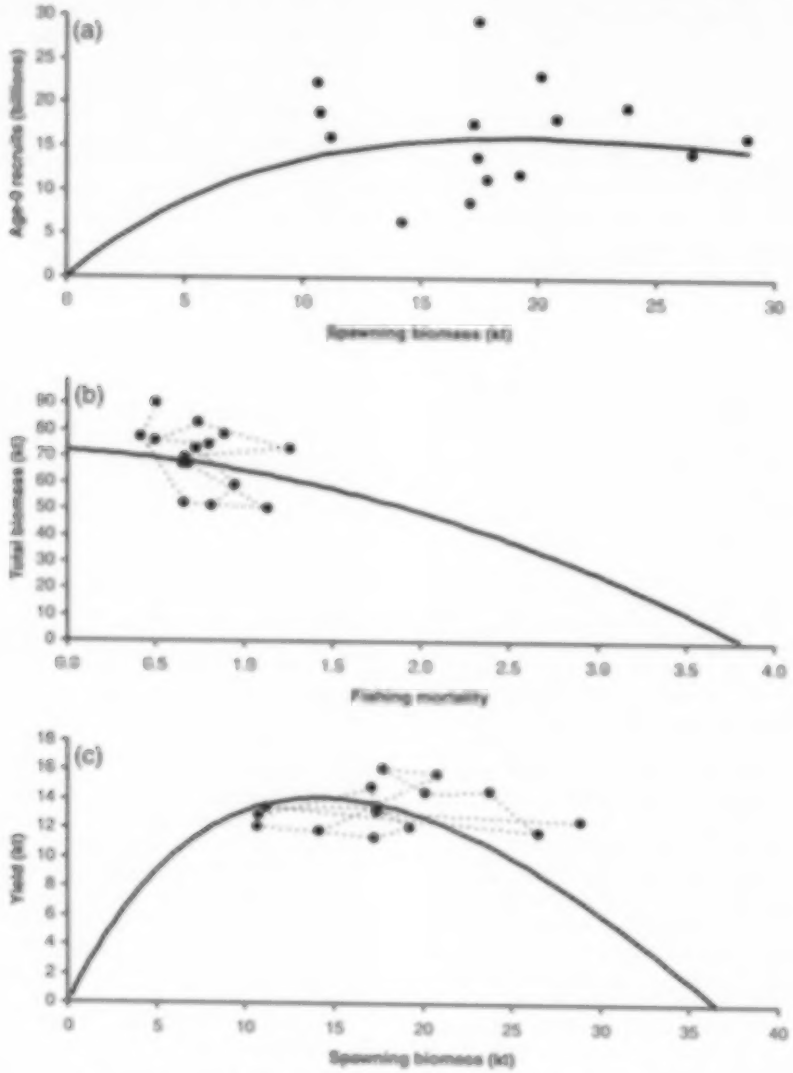
Fig. 11. Demographic production model results for Norwegian Deeps and Skagerrak shrimp, *Pandalus borealis* (circles connected with broken lines indicate the historical series of observations, solid line is the equilibrium expectation; based on provisional assessment results from ICES 2001).



tion to evaluate performance of management based on conventional reference points and the traffic-light approach. Fu et al. (2000) simulated the Kachemak Bay shrimp stock to suggest that a biomass threshold is not needed if constant recruitment is assumed. However, they concluded that a biomass threshold is needed to avoid stock collapse if a stock–recruitment function is included. They therefore concluded that assuming constant recruitment for Kachemak Bay shrimp is risky. Martell et al. (2000) used a variety of simulation modeling to examine alternative management options for a *P. jordani* stock off the west coast of Vancouver Island and recommended target reference points based on a fixed exploitation rate (35%) of surplus population above a limit reference point based on minimal biomass (1000 t).

Some aspects of Pandalid life history, such as temporal and spatial segregation and co-occurrence of the sexes (Barr and McBride 1967; Shumway et al. 1985; Boutillier and Sloan 1988), can best be examined with population simulators. Simulations can evaluate alternative harvesting strategies (seasons, closed areas, etc.), interaction with overlapping predator populations, and environmental responses. For example, Fox (1973) discusses the potential egg loss due to trawling on spawning aggregations of shrimp.

Long-term simulations can determine consistent F and stock size reference points. For example, management of Norwegian Deeps and Skagerrak shrimp is based on maintaining SSB well above B_{lim}, and stochastic simulations suggested that the risk of the stock decreasing to less than B_{lim} was low if the stock was fished at F_{med} (0.65; ICES 2000). Therefore F_{med} would be a target that is consistent with the limit biomass reference point. Stock size reference points can also be determined by long-term simulation, based on

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the projected stock size maintained by a desired F reference point.

One disadvantage of demographic production models is the typical assumption of fixed population parameters such as maturity, growth, and natural mortality rates. Usually the only density dependence included in demographic production models is in the stock–recruitment relationship. Similar to dynamic pool estimators, assuming no density-dependent compensation in other life history traits may compromise the realism of models but can be considered to be risk averse.

A hierarchical approach to limits and default precautionary targets

According to the tiered approach to reference point estimation, reference points are determined by the method that most reliably captures important population and fishery dynamics, which may not be the most advanced model, given the data available from the population and fishery. For example, Abramson and Tomlinson (1972) applied biomass dynamics, YPR, and stock–recruit approaches to California ocean shrimp but concluded that the biomass dynamics model was most appropriate for providing fishery management advice. However, we propose that research should attempt to provide more detailed information so that more advanced models can be applied.

Flemish cap shrimp offers an example of a lower-tier analysis. The fishery is relatively recent (1993) and the research program is based on a relatively short time series of survey observations, evaluating fishery catch rates, and compiling information on basic life history (NAFO 2001). Therefore, management advice is based on catches that appear to maintain stability in survey biomass indices. The NAFO Scientific Council recommended that this descriptive approach should eventually be replaced with more advanced reference point estimates as an analytical assessment develops (NAFO 2001).

An example of a middle-tiered approach is that taken for the assessment of West Greenland shrimp, which has information on yield, fishery catch rates, survey biomass, and predation by cod (Hvingel and Kingsley 2002). Biomass dynamics of West Greenland shrimp conform well to production models and can be used to determine MSY reference points (NAFO 2002). Furthermore, performance of alternative management decisions can be evaluated in the context of maintaining B_{MSY}. Although a biomass dynamics model is being used to assess the status of West Greenland shrimp, Hvingel and Kingsley (2002) advocate the exploration of more informative methods such as delay-difference and age-based methods.

The reference points used to manage Gulf of Maine shrimp provide an example of the dynamic pool approach. Life history and fishery selectivity information are available for an age-based model, and historical biomass dynamics indicate the levels of egg production per recruit for avoiding stock collapse and sustainability. However, the age-based model can be advanced with better information on discrete growth and protandry. Furthermore, information on stock and recruitment (in absolute units rather than in relative survey units) would allow exploration of demographic production models.

There are few examples of shrimp reference points based on more advanced approaches. One assessment that approached the top tier of reference point methods was Norwegian Deeps and Skagerrak shrimp, which had a series of spawning biomass and recruitment observations, as well as the life history and partial recruitment necessary for an age-based production model. For example, stochastic simulation could be used to determine the level of F that would maintain a stock above the lowest observed stock size (ICES 2000). However, the age-based assessment was abandoned in favor of a production model with predation and recruitment terms because of the uncertainty in age determination and the importance of predation (ICES 2001). This example suggests that the simple population model may be the most appropriate approach for determining reference points if abiotic or multispecies factors are the most important factors influencing productivity.

A precautionary approach to managing Pandalid fisheries requires estimates of limit reference points as well as variance estimates for determining precautionary targets for all Pandalid resources (Prager et al. 2003). Variance of historical proxies can be based on the estimation variance of historical stock size or F. Estimates of variance for MSY reference points from biomass dynamics models are typically from bootstrap (e.g., Prager 1994), jackknife (e.g., Hvingel and Kingsley 2000), or Bayesian methods (Hvingel and Kingsley 2001, 2002). Variance of dynamic pool reference points can be derived from Monte Carlo methods (e.g., Restrepo and Fox 1988). Variability of reference point estimates from stock–recruit or demographic production models can be derived by bootstrapping stock–recruit observations (e.g., Overholtz 1999). The variance of reference points is considered in several precautionary-approach frameworks. For example, ICES typically determines a precautionary reference point as a function of the variance of the limit reference point estimate (ICES 1997).

Unfortunately, lower-tier approaches (e.g., historical proxies) do not include variance estimation, and middle-tier approaches (e.g., biomass dynamics models) often underestimate the actual uncertainty in reference point estimates. Therefore, a more qualitative consideration of uncertainty is needed for data-poor applications. For example, Restrepo et al. (1998) advocate default targets (e.g., 75% of limit F) in data-moderate or data-poor situations. The use of interim reference points and default targets, with continued advancement of methodological applications, is a precautionary approach to management of Pandalid shrimp resources.

To insure that conservation goals are met, it is critically important to understand the stock–recruitment process if we are truly going to effectively manage stocks and prevent recruitment overfishing. It is easy to conclude that there is no stock–recruitment relationship; the challenge before us is to continually question and improve our assessment methodologies and model against our ever-changing understanding of the biotic and abiotic factors affecting all life stages of these animals and the environments in which they live. For example, research should be promoted to provide or maintain reliable estimates of stock and recruitment. Despite the challenge imposed by environmental influences, reference points for Pandalid shrimp should be estimated. Studies that have tested environmental effects on shrimp productivity, either

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abiotic factors (Richards et al. 1996; Koeller 2000) or predation (Lilly et al. 2000), have also indicated a significant effect of shrimp population size. In lieu of the information required by advanced approaches to estimating reference points, interim reference points or proxies should be determined, and a framework should be developed to systematically collect the missing information similar to the phased approach recommended by Perry et al. (1999).

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PERSPECTIVE / PERSPECTIVE

Biological reference points for American lobster (*Homarus americanus*) populations: limits to exploitation and the precautionary approach[1]

Michael J. Fogarty and Louise Gendron

Abstract: Large-scale changes in American lobster (*Homarus americanus*) landings and abundance have been documented in both Canada and the United States over the last several decades. The spatial coherence of these changes suggests the importance of common environmental and fishery-related factors operating over broad areas in the western North Atlantic. Changes in both biotic and abiotic factors have been hypothesized to underlie the recent increases in lobster production. Area expansion of lobsters to previously unoccupied or low-density areas appears to be an important element of the population increase. Here, we review biological reference points applied to American lobster populations in the United States and Canada. Egg production per recruit models have been used to specify limit reference points ($F_{10\%}$ in the United States) or target reference points (increasing egg production per recruit to twice its 1995 level in Canada). Surplus production and yield-per-recruit models have also been employed to provide qualitative management guidelines. We describe sources of uncertainty in the development of biological reference points for American lobster based on dynamic pool models in relation to the precautionary approach. Finally we consider auxiliary indicators and reference points with potential application to lobster stocks.

Résumé : On a observé durant les dernières décennies, tant au Canada qu'aux États-Unis, des changements à grande échelle dans les débarquements et l'abondance du homard d'Amérique (*Homarus americanus*). La concordance de ces changements dans différentes régions laisse croire que des facteurs communs reliés à l'environnement ou à la pêche agissent sur de grandes surfaces de l'ouest de l'Atlantique Nord. On a émis l'hypothèse que des changements dans les facteurs abiotiques et biotiques expliquent les accroissements récents de la production de homards. L'extension d'aire des homards dans des régions antérieurement peu ou pas occupées semble être un élément important de l'accroissement de la population. Nous examinons les points de référence biologiques utilisés pour les populations du homard d'Amérique aux États-Unis et au Canada. Des modèles de production d'oeufs par recrue ont servi à déterminer des points de référence limites ($F_{10\%}$ aux États-Unis) et des points de référence cibles (accroissement de la production d'oeufs par recrue au double de sa valeur en 1995, au Canada). Les modèles de production excédentaire et de rendement par recrue ont aussi été utilisés pour fournir des règles qualitatives de gestion. Nous décrivons les sources d'incertitude dans le développement de points de référence pour le homard d'Amérique basés sur des modèles analytiques en relation avec le principe de précaution. Nous examinons finalement des indicateurs et des points de référence auxiliaires qui pourraient s'appliquer potentiellement aux stocks de homards.

[Traduit par la Rédaction]

Introduction

The American lobster (*Homarus americanus*) has supported important commercial fisheries on the eastern seaboard of North America since the early nineteenth century. The lobster resource is consistently ranked among the most valuable fishery commodities in Canada and the United States. Reported lobster landings are currently at or near historically high levels in both countries (Fig. 1). Annual exploitation rates are high, with current estimates often

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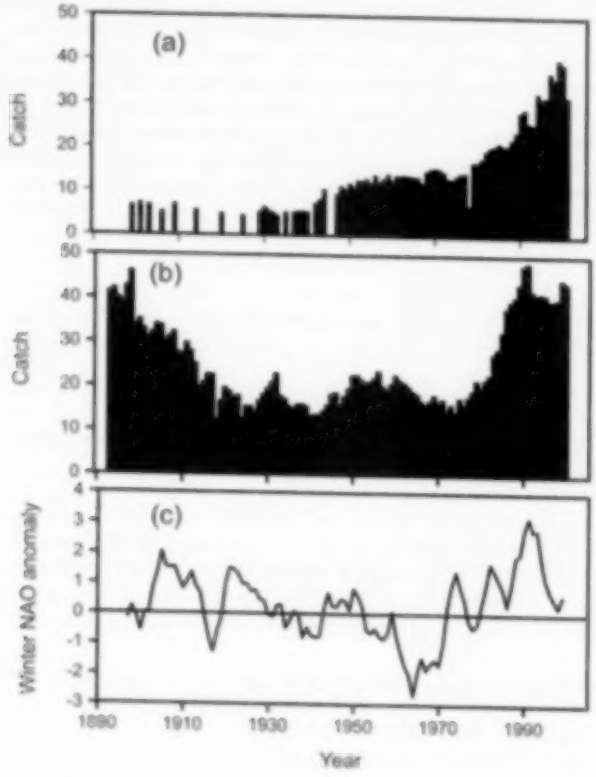
Fig. 1. Trends in landings (thousand metric tons) of American lobster in (*a*) the United States and (*b*) Canada and (*c*) the winter North Atlantic Oscillation (NAO) index. The NAO index is smoothed using a low-pass filter.



exceeding 80% (Fisheries Resource Conservation Council (FRCC) 1995; Fogarty 1995; Atlantic States Marine Fisheries Commission (ASMFC) 2000*b*). The apparently high resilience of American lobster stocks to exploitation (see Fogarty (1995) for stock status) has been linked to the existence of spatial refugia and larval source–sink dynamics (Anthony and Caddy 1980; Fogarty 1998), the nature of the stock–recruitment relationship, and lobster life history characteristics (Caddy 1986; Fogarty and Idoine 1986; Ennis and Fogarty 1997). Dramatic increases in lobster landings, most notably during the 1980s and 1990s, appear to be related to changes in fishery characteristics and shifts in environmental and ecological conditions affecting production levels (Fogarty 1995; ASMFC 2000*a*, 2000*b*). Recent sharp declines in landings in the southern New England region and reduced landings in some Lobster Fishing Areas in Canada highlight the need to understand the factors resulting in shifting lobster production domains.

The American lobster has traditionally been managed through input controls, including limitation of fishing effort or fishing activity and controls on the size and reproductive condition of lobsters taken (Miller 1995; Annala and Sullivan 1997). The rationale for these management measures has been based principally on yield-per-recruit (YPR) considerations, attempts to conserve the breeding population, and marketing factors. Output controls such as quotas have not been used as management tools to date, except in one fishing area off southern Nova Scotia. In Canada, regulation of fishing effort includes controls on the number and type of traps, the number of licenses holders, and the duration of the fishing season. In the majority of the areas, no new licenses have been granted since the beginning of the 1970s (Miller 1995). Despite these tight controls, nominal fishing effort is nevertheless considered too high (FRCC 1995). Moreover, effort regulations did not prevent important increases in the effective fishing effort over the last two or three decades (e.g., Gendron and Archambault 1997). In the United States, the lobster fishery has traditionally been an open-access fishery and trap limitations and some forms of access restriction have only recently been implemented.

Here, we review applications to date of biological reference points (BRPs) for American lobster populations in the United States and Canada and provide a perspective on American lobster management in the context of an apparent regime shift (sensu Steele 1998) in lobster production. We examine the underlying conceptual foundations of the BRPs applied to lobster, explore important sources of uncertainty in the determination of limit BRPs, and describe cases where risk analysis has been used to cope with uncertainty. We discuss the implementation of a precautionary approach (PA) and address specification of alternative BRPs currently under consideration in American lobster stocks. Finally, we explore the applicability of alternative management tools for meeting conservation objectives.

Lobster BRPs

Early development of BRPs for American lobster populations was based on application of surplus production and dynamic pool models. These reference points, however, have been principally used as qualitative guides for lobster management rather than negotiated targets or limits used to trigger a specified sequence of management actions.

Examination of yield–effort relationships have provided the basis for general recommendations concerning the desirability of reductions in overall levels of fishing effort in lobster fisheries in the United States (e.g., Halgren 1980; Fogarty and Murawski 1986; Jensen 1986). Surplus production models have been applied as a basis for management for other lobster taxa including rock lobster (*Jasus edwardsii*) (Saila et al. 1979; Booth and Breen 1994) and western rock lobster (*Panulirus cygnus*) (Hall and Brown 1994). Fogarty (1995) demonstrated a shift in the yield–effort relationship for the Maine fishery during the last several decades. Although caution is necessary in interpreting the available catch and effort series, the change suggests the possibility that an altered and nonstationary production domain now exists in this fishery. The change may be the result of alteration in ecological or environmental conditions, changes in fishery characteristics, or both (Fogarty 1995). The implications for shifts in production characteristics for BRPs are addressed more fully below.

YPR considerations have played a central role in the development of lobster management advice in both Canada and the United States including recommendations for reductions in fishing mortality rates and changes in minimum legal size limits (e.g., Ennis 1980; Fogarty 1980; Campbell

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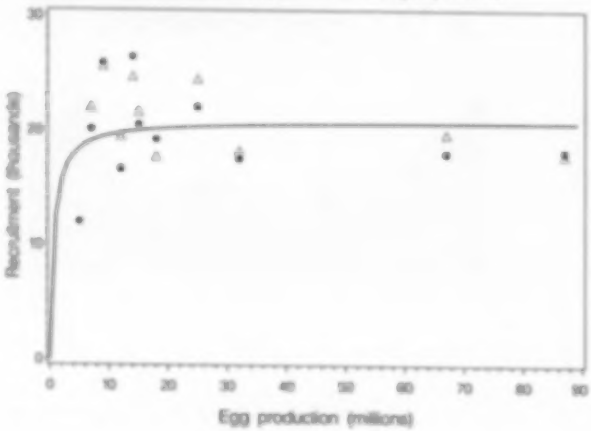
1985). American lobster assessments consistently indicate high levels of fishing mortality on inshore populations and that increases in YPR and (or) economic efficiency would result under reductions in exploitation rates and increases in minimum size limits (e.g., Ennis 1980; Fogarty 1980; Campbell 1985). Again, in all cases, however, these analyses have been used as qualitative guides to regulatory action rather than as hard targets despite clear indications of growth overfishing based on YPR considerations.

In the last decade, egg production per recruit (EPR) reference points have formally been adopted in both the United States (New England Fishery Management Council (NEFMC) 1995; ASMFC 2000*a*, 2000*b*) and Canada (FRCC 1995). In the United States, a reduction in EPR to 10% of the unexploited state has been implemented as a management limit (NEFMC 1995; ASMFC 2000*a*, 2000*b*). In Canada, a goal of doubling EPR relative to 1995 levels has been adopted as a management target (FRCC 1995). The possibility of implementing a 5% limit EPR reference point in Canada is currently under consideration. In both countries, EPR is currently calculated using extensions to the Fogarty and Idoine (1988) model (Gendron and Gagnon 2001; J. Idoine, National Oceanic and Atmospheric Administration, Fisheries, 166 Water Street, Woods Hole, MA 02543, USA, personal communication; D. Pezzack, Department of Fisheries and Oceans, Bedford Institute of Oceanography, P.O. Box 1006, Halifax, NS B2Y 4A2, Canada, personal communication).

The definition of a limit reference point based on EPR considerations is linked to the rate of recruitment at low levels of population egg production. Given information on the slope of the recruitment curve at the origin and an analysis of EPR for a specified fishery selection pattern, an estimate of the limiting level of fishing mortality for the stock can be defined. The EPR limit reference point applied to the American lobster was implemented without definitive information on the slope of the recruitment curve at the origin. In the United States, the choice of the $F_{10\%}$ level was based on metaanalyses of the slope of the recruitment curve at the origin for a number of marine species (e.g., Mace and Sissenwine 1993) with further qualitative consideration of lobster life history features. Fogarty and Idoine (1986) and Ennis and Fogarty (1997) provided indications that the slope of the lobster recruitment curve at the origin is relatively steep (Fig. 2), consistent with the apparently high resilience to exploitation exhibited by this species.

The application of limit reference points for lobster stocks has been controversial because of the perceived mismatch between the apparent health of the resource as indicated by high landings and recommendations to take remedial action indicated by low levels of estimated EPR. In part, the controversy is also due to the misapprehension that the EPR models "predict" a stock collapse. The overall controversy must be viewed in the context of an apparent shift in lobster production rates over the last several decades. Nonstationarity in production dynamics of exploited aquatic resources on decadal and multidecadal time scales can be expected (Walters 1987) and may require adjustment in reference points and (or) management strategies. Preferably, BRPs should be sufficiently robust to accommodate a range of environmental and ecological conditions. Strategies for coping with low-frequency shifts in the environment and

Fig. 2. Relationship between population egg production and recruitment to the adult population in Arnold's Cove, Newfoundland. Recruitment has been estimated using a protracted recruitment pattern (Sheehy 2001) in which recruitment occurs over the ages 8–11 (triangles). The proportion recruiting at age represents a modification of the schedule considered by Sheehy (2001) with p_8 = 0.15, p_9 = 0.45, p_{10} = 0.25, and p_{11} = 0.15. The modification consolidates the partial recruitment pattern of Sheehy (2001) by grouping recruitment for ages 7 and 8 and ages 11 and 12 into single age groups. The smooth curve is the recruitment function determined by Ennis and Fogarty (1997). The circles are the original recruitment indices used by Ennis and Fogarty 1997).



production were evaluated by Walters and Parma (1996) and MacCall (2001). The uncertainty related to identifying and predicting these shifts in productivity is a major issue in lobster risk assessment and management.

Reference points and environmental variability

The trend in increasing lobster landings in both the United States and Canada through the 1980s and 1990s can be attributed, in part, to a number of fishery-related factors including overall increases in fishing effort, expansion of the fishing grounds to include offshore and deeper water sites that may have served as de facto refuge areas, changes in gear and overall technological efficiency, increases in the minimum legal size in some areas, increased compliance with regulations such as minimum legal size limits and protection of ovigerous females, and more complete reporting of landings (for a detailed review, see Fogarty 1995). In the Canadian fishery, where effort is controlled, increase in landings is partly attributed to improvements in fishing efficiency brought by technological changes (e.g., Gendron and Archambault 1997).

The change in landings is also related to an apparent increase in abundance. The geographical scale of the recent increase suggests common underlying environmental or ecological factors operating over broad regions. Changes in physical environmental factors and in predation levels have been proposed as potential mechanisms underlying the increase in recruitment and abundance (for a review, see Fogarty 1995). An expansion of the population(s) into habitats with low

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shelter availability and structural complexity has also been suggested. Anecdotal information from fishers indicates the presence of lobsters on grounds where traditionally no lobsters were found (e.g., Archambault 1997). In the United States, the clearest evidence for population increases is derived from bottom trawl surveys (ASMFC 2000*a*), which sample most effectively on soft-substrate habitats that were previously characterized by low density.

A shift in biotic and (or) abiotic conditions affecting survival rates during the early life history stages has direct consequences for the specification of limit and target reference points. For example, a change in the density-independent mortality rates during the early life stages will principally affect the rate of recruitment at low egg production levels, thereby influencing the limiting level of fishing mortality (F_T) at which the risk of a population collapse is high. The relationship between egg production (E) and recruitment (R) can be expressed as

$$R_t = \alpha f(E_{t-r})$$

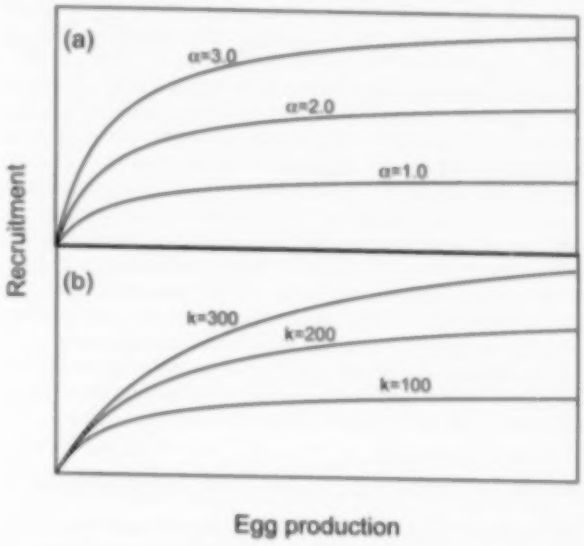
where α is the rate of recruitment at low egg production levels, r is the delay between spawning and recruitment, and $f(E_{t-r})$ is a compensatory function. For the American lobster, empirical evidence (Fogarty and Idoine 1986; Ennis and Fogarty 1997) (see Fig. 2) and theoretical considerations (Caddy 1986) suggest an overall asymptotic relationship between egg production and recruitment. One possible compensatory function for this relationship is

$$f[E_{t-r}] = \frac{E_{t-r}}{1 + E_{t-r}/k}$$

where k is the population egg production level above which density-dependent factors dominate (see Shepherd 1982). The estimate of F_T is given by the fishing mortality rate for a given age- or size-selective pattern of fishing that results in a level of EPR equal to α^{-1}. Accordingly, any factor that results in sustained shifts in α through changes in density-independent mortality rates will directly affect the appropriate choice of F_T (Fig. 3*a*). An increase in α will result not only in an increase in the overall recruitment level but also in an increase in the resilience of the population to exploitation. In contrast, factors affecting the density-dependent component will principally result in changes in the asymptotic recruitment level (Fig. 3*b*). If habitat suitability and (or) availability has increased or habitat types occupied have changed, overall increases in recruitment and abundance could occur even if bottlenecks (Wahle and Steneck 1991) were previously important in hard-substrate environments.

Reductions in fish predators through overharvesting have been suggested as one potential mechanism underlying an increase in lobster recruitment. Reduction in predatory fish populations has been linked to higher abundance levels of other crustacean populations in the Northwest Atlantic (e.g., Witman and Sebens 1992; Worm and Myers 2003). A potential role of declining Atlantic cod (*Gadus morhua*) predation on lobster populations has also been posited (Jackson et al. 2001), although Hanson and Lanteigne (2000) concluded that changes in predation rates by cod on lobster in the Gulf of St. Lawrence could not account for changes in landings in this region. The potential role of other predators has not been fully explored.

Fig. 3. Effect of changing (*a*) the rate of increase in recruitment at low egg production levels and (*b*) the egg production level at which density-dependent processes dominate for a Shepherd stock–recruitment model.



Changes in large-scale climatic conditions in the North Atlantic have also been identified. For example, the winter North Atlantic Oscillation (NAO) index exhibited a generally increasing trend from the early 1970s to the mid-1990s (see Fig. 1). Changes in the NAO potentially affect wind fields, temperature patterns, and precipitation over the North Atlantic. In turn, these factors can potentially affect larval transport, individual growth, and ecosystem productivity. Drinkwater et al. (1996) examined temperature-related effects on lobster landings and concluded that the recent increases in landings cannot be attributed to increasing water temperatures alone. Information on NAO effects on larval transport and ecosystem productivity is not currently available. It is likely that the increase in lobster abundance reflects the interplay of a number of fishery-related, abiotic, and biotic factors. One or more of these factors may be dominant during different time periods. With respect to defining lobster BRPs, the key issue remains to determine whether environmental changes have affected density-dependent or density-independent factors (or both).

The effects of environmental variability on recruitment dynamics represent an important source of uncertainty in the specification of the form of the relationship between egg production and recruitment and the slope of the recruitment curve at the origin. This has practical implications in establishing limit reference points for American lobster; the current EPR-based limits may seem too conservative in periods of high productivity but may not be conservative enough under adverse conditions.

Ennis and Fogarty (1997) noted that the available population time series for Arnold's Cove is drawn from a period of high landings (and high population size relative to the previous two or three decades) and may reflect unusually favor-

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able conditions for recruitment. If density-independent mortality rates were lower during the period of observation, the slope of the recruitment curve would be higher than under less favorable environmental conditions and would imply a higher resilience to exploitation. Ennis and Fogarty (1997) noted that indication of a steeply ascending limb of the egg production – recruitment relationship is not a justification for allowing high levels of fishing mortality. Although the form of the relationship between egg production and recruitment for Arnold's Cove is not an artefact as suggested by Sheehy (2001) (see Fig. 2), several important sources of uncertainty remain. Ennis and Fogarty (1997) noted that it is not known if this stock can be considered a closed population. Larval or juvenile input from exogenous sources would affect inferences on the form of the egg production – recruitment relationship. In particular, inferences concerning the rate of recruitment at low egg production levels would be affected. These sources of uncertainty must be strongly considered in any attempt to use the extant information on the egg production – recruitment relationship directly to set limit reference points.

Uncertainties in EPR and risk assessment

Two main sources of uncertainty must be examined in the determination of limit reference points: the estimation of EPR for a virgin population and the variability in parameters used in the assessment of EPR. In the United States, the limit EPR reference point is expressed as a percentage of the EPR when $F = 0$. Lobsters have an extensive history of exploitation in coastal waters and virgin stock conditions are not known. Furthermore, information is not currently available on whether density dependence exists in growth, maturation, and natural mortality of recruited lobsters. Accordingly, concern has been expressed about standardizing EPR to unexploited conditions. In recognition of these concerns, a goal of doubling EPR relative to recent (1995) levels was adopted in Canada in preference to a limit reference point expressed as a percentage of the estimated maximum egg production level under the assumption of no density dependence. The strategy underlying the $F_{10\%}$ level in the United States with its implicit assumption of no density dependence in growth and reproduction is appropriately viewed as an application of a risk-averse reference point, since it will yield more conservative results than corresponding analyses incorporating density-dependent processes. However, uncertainties in growth rates, reproductive patterns, and factors such as egg and larval viability of progeny produced by larger, older lobsters become increasingly important when results are expressed in reference to the unexploited case.

The model-based EPR reference point relies on a number of parameters subject to uncertainty. Calculation of EPR production integrates every component of the annual cycle of the recruited lobster (natural and fishing mortality, molt increment and molt frequency, size at sexual maturity, fecundity and reproductive cycle). All of these parameters are subject to considerable process and measurement uncertainty. Quantitative expression of uncertainties and its translation into probabilistic statements of reaching a given target or falling below a limit are the basis of explicit risk evaluation. Although risk analysis has been broadly applied to fish stocks, application to American lobster populations has only recently been attempted. Gendron and Gagnon (2001) provided an evaluation of management risk (the probability of not achieving a management target (doubling of EPR)) following the implementation of a number of different management actions. Management actions examined include measures such as increasing the minimum legal size from its initial value of 76 mm carapace length. Uncertainty functions were attributed to the parameters of the EPR model, and propagation of uncertainty to the final estimates of EPR production was done using Monte Carlo simulations. EPR values were then expressed relative to the estimated values of EPR before the implementation of new management measures. The ratio between the two values, referred to as the increment factor, was used to determine which management scenarios can, at least in theory, achieve the objective of doubling EPR (an increment factor of 2). Cumulative frequency distribution of the EPR increment factor values obtained from 100 iterations were computed and used for assessing the management risk, i.e., the probability of not reaching an increment factor of 2, corresponding to the management target of doubling EPR. An example is provided for the Magdalen Islands fishery (Quebec) for different minimum legal sizes (Fig. 4). From the analysis, a management plan including an increase in minimum carapace length from 76 to 83 mm, 1 mm each year from 1997 to 2003, was agreed upon and implemented to reach the target of doubling EPR. Probability curves proved useful to illustrate to stakeholders the uncertainty in the evaluation of EPR production and the management risk associated with a given management action. To date, however, there has been no real discussion on what could be considered an acceptable level of management risk. In this example, the management measure of increasing carapace length was set not to go beyond a 50% risk of not reaching the target.

Chen and Wilson (2002) provided an evaluation of the biological risk of overfishing by comparing the current level of exploitation (F_{cur}) with the level of fishing mortality that reduces EPR production to 10% of its maximum, i.e., that produced in the absence of a fishery ($F_{10\%}$), corresponding to the limit reference point currently used for the American lobster in the United States. Methodology to quantify uncertainty in the assessment of $F_{10\%}$ was similar to the one described above where uncertainty functions were attributed to the parameters of the EPR model. Propagation of uncertainty was evaluated using the Monte Carlo method. Chen and Wilson (2002) employed assumed levels of variability in the input parameters of the EPR model. Five levels of uncertainty were used in the simulations. Uncertainty in F_{cur} was based on bootstrapped estimates from a DeLury analysis (ASMFC 2000*b*). Probability distribution functions of estimated values of F_{cur} and $F_{10\%}$ were superimposed and the risk that the current fishing exceeds the limit reference point of $F_{10\%}$ was determined by the degree of overlap of the two probability distribution function curves following a stochastic decision-making framework developed by Helser et al. (2001). The authors concluded that the uncertainties do not permit a definitive conclusion that the lobster resource is overfished in the Gulf of Maine. Chen and Wilson (2002) noted that work is still needed to accurately determine stock status in relation

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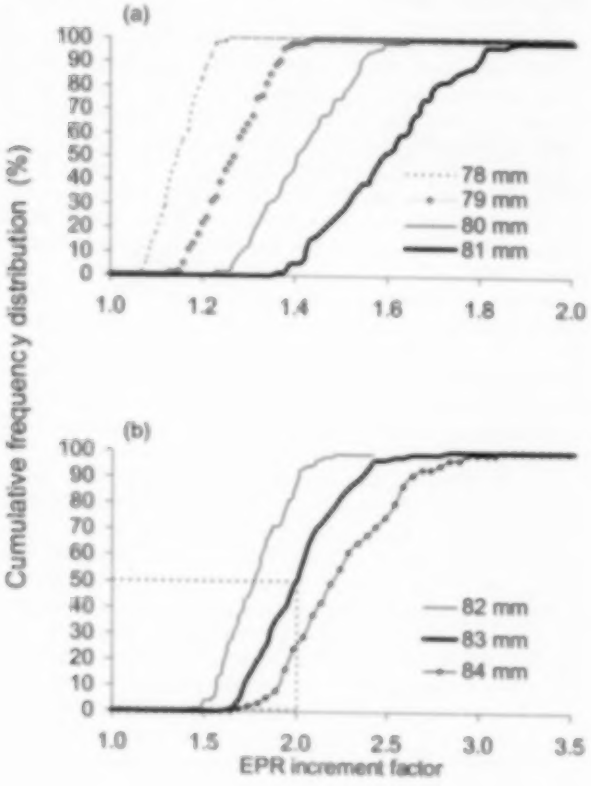
Fig. 4. Cumulative frequency distribution of the 100 EPR increment factor values obtained from Monte Carlo simulations. The increment factor corresponds to the ratio of EPR calculated for a given management measure to EPR calculated before its implementation. In this example, different increases in minimum legal size to (*a*) 78- to 81-mm carapace length and (*b*) 82- to 84-mm carapace length from an initial value of 76-mm carapace length are examined for the Quebec Magdalen Islands fishery. The percentage of EPR increment factor values <2 illustrates the management risk, i.e., the probability of not reaching the management target of doubling EPR under the management scenario tested.



to the EPR limit reference point and, more specifically, approaches to reducing uncertainty in the estimates of current fishing mortality. Sensitivity analysis could complement these types of studies to determine the relative importance of the different parameters in the uncertainty in the overall EPR estimates. Chen and Wilson (2002) presented a decision-making framework; however, standard guidance on the utilization of confidence and risk levels remains to be specified to derive solid interpretations on the status of the stock.

Uncertainties still remain concerning the female life cycle. A recent study by Comeau and Savoie (2002) in the southern Gulf of St. Lawrence indicated that a significant number of females could spawn in successive years, molt and spawn in the same year, or skip molting or spawning for a year, depending on their size and reproductive status (first-time spawners or multiple spawners). Such features are different from the generally accepted 2-year cycle with molting and spawning in alternate years as described by Aiken and Waddy (1982) for females smaller than 120 mm carapace length and still need to be quantified in many areas and included in the EPR simulation models.

Harvest control rules and the PA

In the United States, a determination that the EPR limit reference point is being exceeded is intended to trigger the establishment of mandated reductions in fishing mortality or other actions to reduce overfishing. In practice, management actions have been deferred in the face of debate concerning the status of the resource. At present, a unidimensional control rule based on fishing mortality reference points is employed in lobster management, where F_{cent} is compared with $F_{10\%}$. Fishing mortality is currently estimated based on a DeLury analysis as noted above (ASMFC 2000*b*).

In the application of a PA to fisheries management, a formal adoption of harvest control rules has been recommended (Food and Agriculture Organization 1996). The PA has now been broadly adopted within international and national management arenas where decisions in fisheries management must be made in situations of high scientific uncertainty. In the United States, principles of the PA in fisheries management are included in the National Standards Guidelines (particularly the Guidelines for National Standard 1) under the Magnuson–Stevens Fisheries Conservation and Management Act (National Oceanic and Atmospheric Administration 1996). In Canada, implementation of the PA is in accord with the framework developed by the Canadian Privy Council Office (Department of Fisheries and Oceans 2002). So far, the PA has not been formally implemented for American lobster. In the PA context, limits are conceived as reference levels that should have a low probability of being exceeded and are designed to prevent stock declines through recruitment overfishing, while targets are used for the determination of harvest control rules that are risk-averse and have a low probability of causing serious harm.

In instances where the limit fishing mortality reference point is exceeded, overfishing is said to occur; when the stock declines below the limit biomass reference point, the stock is overfished. Shifts in ecological and environmental conditions that persist over multiyear periods can, however, result in circumstances where enhanced recruitment occurs, despite systemic overfishing. In these cases, the stock may not be considered overfished even though overfishing is occurring (see Restrepo et al. 1998). A fuller representation of lobster resource status by including measures of biomass, abundance, and other biological characteristics of lobster populations (see alternative BRPs) would permit a distinction between overfishing and the overfished state under prevailing environmental conditions.

An example of a two-dimensional control rule using abundance information derived from fishery-independent and fishery-dependent sources (ASMFC 2000*b*) and the EPR reference point is provided for lobster in the Gulf of Maine (Fig. 5). Abundance and fishing mortality estimates were available for the period 1982–1997 (ASMFC 2000*b*). For illustrative purposes, we have mapped this empirical information against the $F_{10\%}$ limit and a hypothetical limit set at the median of the observed abundance time series (Fig. 5). Un-

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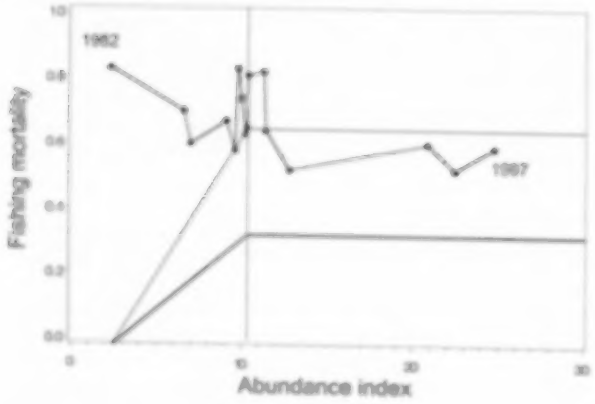
Fig. 5. Two-dimensional control rule utilizing empirical information on abundance and the $F_{10\%}$ EPR reference point. Empirical estimates for the period 1982–1997 (ASMFC 2000*b*) are illustrated (circles) in the control rule phase space. A hypothetical application of an abundance reference point set at the median abundance level and using the existing fishing mortality reference point is illustrated for the control rule (lower line); the upper line illustrates a hypothetical control rule in which the median of both the abundance series and the fishing mortality rate for the period 1982–1997 is used. Lowest acceptable biomass set to lowest observed in series. Control rules based on extant time series must be carefully evaluated for changes in production levels; those depicted are for illustration only.



der this set of possible control rules, overfishing would be considered to occur but the stock would not be classified as overfished in the more recent part of the time series. Such an approach would permit a better representation of stock status and would reflect more fully the apparent increase in recruitment and productivity over this time period. This approach could possibly be used as a basis for the implementation of a PA to lobster management and the determination of relevant control rules. In practice, the choice of limiting fishing mortality rates and biomass levels would ideally be developed in consultation with user groups and used to define a preagreed and accepted sequence of management actions if the stock is determined to be overfished.

In other lobster taxa, multidimensional control rules have been employed. In the spiny lobster (*Panulirus argus*) fishery in Florida, an F_{SPR} control rule is employed in concert with a recruitment indicator; the stock is considered overfished if the F_{SPR} limit is exceeded and recruitment declines for 3 consecutive years (Rosenberg et al. 1996). Starr et al. (1997) employed a decision rule approach based on trajectories of catch-per-unit-effort for the New Zealand rock lobster. Similar approaches can be employed using alternative measures of abundance or stock condition for American lobster.

Ideally, biological reference limits should be robust enough and remain conservative under different production regimes. However, in practice, when changes in production characteristics occur and persist over extended time frames, it may be necessary to adjust BRPs and control rules. Harvest control rules for a hypothetical situation in which both the slope of the recruitment curve at the origin and the egg production level at which density dependence dominates are increased under favorable environmental conditions relative to unfavorable states of nature are depicted in Fig. 6. If the factors leading to enhanced recruitment are not fully understood and cannot be predicted, however, a substantial source of uncertainty (and controversy) is introduced into the management process. The risk to the resource is high if reference points are set to reflect favorable environmental conditions and the environment subsequently shifts to a lower productivity domain.

Alternative BRPs

In addition to the BRP mentioned above, additional or alternative measures based on demographic characteristics and other features of lobster populations could also be specified. A blend of model-based reference points such as EPR and empirical measures of stock condition can provide an effective approach to the evaluation of stock status (see Caddy 2003). The former can provide an important basis for proactive management, while the latter are firmly grounded in current resource status and can be readily communicated to stakeholders.

Alternative reference points are presently being considered in Canada in support of the conservation objectives expressed by the FRCC (1995). Aside from increasing egg production, another objective stated by FRCC is to enhance the size structure of lobster populations. Presently, most lobster fisheries are dependent on newly recruited animals and populations are characterized by highly truncated size frequency distributions (e.g., Gendron and Savard 2003). Even if the target of doubling EPR has theoretically been reached in some Canadian fishing areas by an increase in minimum legal size, the size structures of the exploited populations still remain sharply compressed (Gendron and Savard 2003). Moreover, increasing minimum legal size without any reduction of fishing effort or other controls on fishing mortality may have undesirable effects. Increasing minimum legal size will increase the number of reproductive females. However, since berried females are protected from the fishery, the greater protection afforded to females compared with males can potentially result in an asymmetry in exploitation rates between males and females. As a result, the sex ratio can be affected and the number of large males could be further reduced if other protections are not implemented. Decreasing abundance of larger males could lead to sperm limitation. This phenomenon has been observed previously in rock lobster and spiny lobster (MacDiarmid and Butler 1999) where females were observed to produce smaller clutches when mated with smaller males. Research is now under way on the American lobster's copulatory system to determine whether this species also shows a potential for sperm limitation. In a laboratory mating experiment, Gosselin et al. (2003) showed that similarly sized females accumulated more ejaculate when mated with large males compared with small males. Moreover, examination of the receptacle load of females in the wild from a heavily exploited population suggests that they were mating mainly with small males. The question of whether ejaculate may actually be limiting to females in the field is still unanswered, but these first observations warrant further research (Gosselin et al. 2003).

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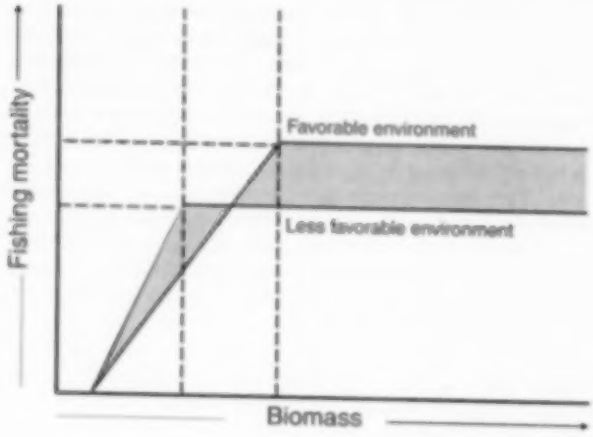
Fig. 6. Two-dimensional control rule based on fishing mortality and biomass (above an acceptable limit) under two sets of environmental conditions. The shaded area represents the region where differences in reference points exist under favorable environmental conditions and under less favorable environmental conditions affecting both the slope of the recruitment curve at the origin and the level of egg production beyond which density dependence dominates. Broken lines represent possible reference levels for fishing mortality and biomass under the two sets of environmental conditions.



Increases in minimum legal size reduce fishing pressure on immature lobsters and thus increase the contribution of eggs by first-time spawners. Recent studies on maternal effect on egg size and quality and larval growth by Ouellet et al. (2003) have shown that in the Gulf of St. Lawrence (Magdalen Islands), larvae (stage I) from first-time spawners were significantly smaller than larvae from larger females (assumed to be multiparous). Additional observations suggest also that larger larvae grow more efficiently. Although substantial heterogeneity within size groups was observed, it is suggested that all of these characteristics may indicate better survival potential of larvae produced by multiparous spawners. The current absence of control of fishing mortality on larger animals will not favor the increase of the contribution of multiple spawners to egg production in this area.

In addition to the EPR reference point, Powles (2001) suggested a reference point based on a ratio of multiparous to primiparous spawners to ensure that a given minimum percentage of egg production is produced by multiple spawners. Similarly, a reference point based on sex ratio could also be developed to prevent any problem of sperm limitation.

In the United States, the overfishing definition adopted by the NEFMC (1995) did in fact include additional measures in addition to the EPR reference point. The full definition is as follows:

> The American lobster is considered recruitment overfished when, throughout its range, the fishing mortality rate (F), given the regulations in place at the time under the suite of regional management measures, results in a reduction in estimated egg production per recruit of 10% or less of a non-fished population.
>
> The development of the status of the stock report and the evaluation of fishery induced effects will consider information based on one or more indices but not limited to: a) Larval abundance index in surface waters; b) larval settlement index (the relative success of each new year class in reaching the benthos); c) pre-recruit indices by year class; d) landings; e) size composition of the landings; f) spawning stock biomass; g) numbers of egg-bearing females; h) effort levels and catch-per-unit-effort and i) possible development of relationships of biological parameters to water temperature or other environmental parameters.

The measures identified in the second section of the NEFMC overfishing definition have also been considered in Canada (Caddy 2001; Department of Fisheries and Oceans 2001). Such measures have not been fully used in assessing the status of the resource, in part because clear limit or target reference points based on these elements have not been defined (Restrepo et al. 1998). However, the potential to enhance the biological bases on which management decisions are made argues strongly for further development of these ideas.

Caddy (2003) argued strongly for a data-based approach as an alternative or in addition to model-based approaches to the determination of BRPs (also see Hilborn 2002). Caddy suggested that greater reliance should be placed in simple and direct observations of population characteristics that are meaningful in terms of population productivity and related to empirical knowledge of limiting conditions or safe-stock situations. For example, Tremblay and Lanteigne (2003) suggested that simple measures of population status such as size at capture relative to size at sexual maturity could constitute simple BRPs that could be emphasized in scientific advice to managers and industry. The traffic light approach could be adopted for the inclusion of such BRPs into scientific advice (Halliday 2000; Caddy 2002).

Management tools

Measures taken in recent years to comply with the EPR target (Canada) or threshold (United States) have mainly been oriented towards increases in escapement (increase in minimum size, implementation of a maximum legal size, a closed-window size, and female v-notching). Although strongly advocated by lobster assessment scientists, direct controls on fishing effort (reduction of the number of licenses and number of traps and reduction of the duration of the fishing season) have encountered some resistance, reflecting social and cultural norms. In Canada, resistance to a reduction of license holders and a limitation of the duration of the fishing season reflects concerns such as maintaining employment in small communities. Concerns over employment opportunities also exist in the US.

Because of the overcapacity of the lobster fishing fleet, fishing effort reductions would have to be drastic to have any significant effect on fishing mortality. Moreover, the benefits of fishing effort reduction on fishing mortality may be variable. The relationship between fishing effort and fishing mortality is governed by catchability, which is rarely

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constant and is known to vary seasonally with life cycle and temperature (for a review, see Miller 1990). Variable catchability will, for instance, generate uncertainty in the outcome of modifications in fishing seasons. This issue has been recently addressed by Gendron and Bréthes (2002) for the Magdalen Islands (Quebec) lobster fishery who showed that reducing the length of the fishing season by closing the fishery earlier was less effective in reducing fishing mortality than delaying the opening of the fishing season because of higher catchability at the beginning of the season. Another issue relates to fishers' behavior who tend to continuously improve their fishing efficiency, particularly when fishing effort reductions are imposed, thus potentially cancelling some of the benefits of reducing the number of traps.

Implementation of controls on fishing effort will have a better chance of success in achieving reductions in fishing mortality if the patterns of fishing effort allocation with respect to resource concentration and movements are well understood. This type of knowledge can eventually help assess the effectiveness of spatial management measures such as closing areas during certain periods of the fishing season. In many areas, patterns of fishing effort allocation have significantly evolved in the last decades in response to technological advances. Fishers are more mobile, cover greater distances, and are more effective at locating lobster. In the Magdalen Islands (Quebec), lobsters are mostly found on offshore grounds at the start of the fishing season (spring) and move closer to shore as the season progresses. Most fishers have adapted their fishing strategy to take into account this movement through a so-called pursuit strategy: fishers will move offshore at the beginning of the fishing season to target lobsters in their wintering grounds and then move their traps inshore to follow concentrations (Gendron et al. 2000). This has resulted in higher fishing mortality, since in the past, not all lobsters would reach the interception site before the end of the fishing season. Gendron and Bréthes (2002) integrated past and current fishing strategies as well as seasonal lobster movement in a two-box spatial model that was used to simulate different tactics of reduction of fishing effort on the overall fishing mortality within a 9-week fishing season. The exercise provided interesting insights into how temporal closures of certain areas could be used as a management tool to reach a given target for fishing mortality. For example, by closing the offshore area at the beginning of the season (first 3 weeks) and then allowing only a small part of the fleet to fish in the offshore area resulted in an 8%–9% reduction in the exploitation rate.

Year-round closures of particular areas for lobster management have not yet been widely implemented. The establishment of fishery closed areas in Bonavista Bay, Newfoundland, has been the most intensively studied case (Rowe 2001, 2002). Two small reserves encompassing a total of 2.1 km^2 were established in 1997; increases in male population density and mean size were observed at both sites (Rowe 2002). An increase in female size and the proportion of ovigerous females was observed at one of the sites. Restricted movements of lobsters resulted in considerable protection afforded to individuals within the closed areas (Rowe 2001). These results suggest that the broader application of year-round fishery closures could be beneficial as a tool in lobster management, particularly where direct controls on fishing effort are difficult to implement. Sizes of reserves would, however, need to be adjusted in relation to local lobster movement patterns. Lobsters can potentially disperse over larger areas than those observed in the Newfoundland closed areas (see Lawton and Lavalli 1995).

Fogarty (1998) examined the potential importance of dispersal processes in a simple discrete space – discrete time model to explore implications for the stability and resilience of lobster populations. The model represented two areas with differential patterns of fishing mortality within each. It was shown that even relatively small rates of exchange potentially confer substantial resilience to exploitation if a source area experiences lower exploitation rates. Although not configured to explicitly represent a marine protected area, these results are directly relevant to the case where fishing mortality in one area is set to zero as in a no-take marine reserve and suggest that the potential benefits of protection of some segment of the population could be significant. The key consideration would rest in identifying important source areas for protection, possibly defined by habitat or other characteristics, while fishing would continue in areas receiving larval subsidies from the closed areas. Specification of the size of the areas required for protection would require further study.

Discussion

A dominant feature of the management environment for American lobster is the uncertainty resulting from an incomplete understanding of the factors affecting recent trends in recruitment and productivity. Threshold or limit EPR reference points that appear to be conservative under prevailing environmental conditions have generated considerable controversy. Although dramatic declines in lobster abundance have recently occurred in the southern portion of the range and these declines have been linked to the combined effects of overfishing, disease, and environmental conditions, the controversy has persisted. It is not currently possible to predict how long the period of enhanced recruitment will last in other areas or whether we will enter a period of lower productivity in these areas. Wahle et al. (2004) documented an overall decline in settlement at two locations in New England during the mid- to late 1990s.

Under these conditions, it would appear prudent to retain a limit reference point for lobster. Indeed, two successive peer reviews of the overfishing definition for American lobster in the United States have advised retention of the EPR reference point as a precautionary measure in the face of uncertainty over whether favorable recruitment will continue (National Marine Fisheries Service 1995; ASMFC 2000*a*). The adoption of a conservative reference point in the context of unpredictable environmental conditions is consistent with a PA to management of this valuable resource. Indeed, it can be reasonably asked whether it will be sufficiently conservative if adverse environmental conditions are encountered in the future. With respect to setting reference points, it is critical to understand whether the population increase was due to density-independent factors affecting survival and growth or density-dependent factors related to overall carrying capacity and habitat expansion.

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A full understanding of the dynamics of lobster populations is complicated by the "shifting baseline syndrome". Large-scale changes in the nearshore abundance of large lobsters and the overall demographic structure of the populations have occurred over more than a century of intensive exploitation (see Fogarty 1995). The sharp truncation in the size composition in inshore components of the population relative to historical demographic characteristics and the consistently high estimates of fishing mortality for lobster populations underlie the concerns for the vulnerability of the resource (Fogarty 1995). These changes affect factors such as the survival probabilities of larval lobsters in relation to size and larval delivery patterns in relation to preferred settlement sites. Further ecological changes in system structure under exploitation may have affected factors such as predation risk, with implications for habitat utilization patterns.

Clear evidence of growth overfishing in virtually all inshore American lobster fisheries suggests the utility of reducing the fishing mortality rates. High fishing mortality rates and resulting reduction in size composition hold important consequences for the lifetime reproductive output of female lobsters. Although the longevity of the American lobster is not known precisely, it is thought to be in excess of 30 years in the absence of exploitation. Presumably, the long life span and large number of potential reproductive events throughout the life cycle are adaptations to variable environmental conditions on decadal time scales. Excessive exploitation interferes with this important reproductive strategy (for a general discussion, see Fogarty 1993). Longhurst (2002) has noted that among fish species, taxa with longer life spans are characterized by higher levels of recruitment variability and that iteroparity is an important evolutionary mechanism for coping with environmental uncertainty. In highly exploited lobster populations, we have imposed a condition approaching functional semelparity. These considerations suggest that BRPs that directly measure factors such as individual female size, male size and numbers, and the number of reproductive opportunities afforded each female, etc., could be important adjuncts to EPR reference points.

It should be noted that BRPs that specify either limiting or target fishing mortality rates would not preclude taking advantage of favorable environmental conditions such as those that apparently prevailed during the 1980s and 1990s. Nor would they necessarily result in foregone yield. Under a fixed exploitation rate strategy, the yield would increase with increasing recruitment. Reductions in fishing mortality rates would further result in YPR benefits. Application of a constant fishing mortality reference point is generally robust to environmental change (Walters and Parma 1996), although there are circumstances where a further adjustment would be required if the rate of recruitment at low population levels declined under unfavorable environmental conditions.

The uncertainty surrounding the factors underlying the apparent increase in production and yield over the last several decades argues for a PA to lobster management. Should environmental conditions shift to an unfavorable regime, levels of exploitation that are now sustainable may then result in stock decline. The inclusion of additional indicators of stock status as BRPs can provide a multidimensional approach for assessing these changes and providing more robust management advice in the face of environmental variability.

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PERSPECTIVE / PERSPECTIVE

Comparison of reference points estimated using a size-based method for two high-latitude crab species in the United States and Canada[1]

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Abstract: We briefly reviewed the decision rules currently used for managing two major high-latitude crab stocks, snow crab (*Chionoecetes opilio*) and Dungeness crab (*Cancer magister*), in the United States and Canada and compared them with model-based reference points, harvest rate, and biomass proportion relative to virgin biomass, developed using species- and area-specific parameters. The model followed a size-based approach, which incorporated Beverton–Holt and Ricker stock–recruitment models and estimated mean and median reference points. The recruitment was also perturbed to generate distributions of reference points. The Beverton–Holt stock–recruitment model provided a lower harvest rate than that of the Ricker model. Harvest rates were lower for combined sexes spawning biomass than for female-only spawning biomass. Increasing the minimum size at first capture and decreasing the handling mortality resulted in increased harvest rates. Changes in fishery duration and timing of fishery open date did not change the harvest rate appreciably. The harvest rates for the Canadian snow and Dungeness crabs were mostly higher than those estimated for the Bering Sea and Southeast Alaska stocks. Reliable estimates of a number of life history parameters are lacking for both species, and hence, the results of this exercise need to be treated in a precautionary manner.

Résumé : Nous examinons les règles de décision couramment utilisées dans la gestion de deux importants stocks de crabes des hautes latitudes, le crabe des neiges (*Chionoecetes opilio*), et le crabe dormeur (*Cancer magister*), aux États-Unis et au Canada. Nous les comparons aux points de référence basés sur des modèles, soit le taux de récolte et la biomasse en proportion de la biomasse vierge, qui utilisent des paramètres spécifiques à l'espèce et au lieu. Le modèle suit une approche basée sur la taille qui incorpore les modèles de stock–recrutement de Beverton–Holt et de Ricker et estime les points de référence moyens et médians. Le recrutement a aussi été modifié afin de produire des distributions de points de référence. Le modèle de stock–recrutement de Beverton–Holt génère un taux de récolte plus faible que le modèle de Ricker. Les taux de récolte sont plus faibles pour la biomasse des reproducteurs des deux sexes combinés que pour la biomasse des femelles reproductrices seulement. L'accroissement de la taille minimale à la première capture et la réduction de la mortalité due à la manipulation augmentent les taux de récolte. Des modifications de la durée de la pêche et de la date d'ouverture ne changent pas de façon appréciable le taux de capture. Les taux de capture du crabe des neiges et du crabe dormeur au Canada sont majoritairement plus élevés que ceux estimés pour les stocks de la mer de Béring et du sud-est de l'Alaska. Nous manquons d'estimations fiables de plusieurs des paramètres démographiques chez les deux espèces; il faut donc considérer les résultats de cet exercice avec circonspection.

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Introduction

Reference points (RPs) are used as benchmarks to assess the status of a stock or stock complex for management purposes. In the United States and Canada, they are defined often in terms of fishing mortality (F) and (or) stock biomass (B). The RPs can be derived by quantitative analysis or assigned an arbitrary value (Caddy and Mahon 1995). The RPs for data- and analysis-rich stocks are determined mostly by rigorous quantitative analysis, whereas RPs for data- and analysis-poor stocks are evaluated by limited quantitative analysis or assigned arbitrary values borrowed from fisheries for similar stocks from other jurisdictions.

Most fisheries are managed with the intention of attaining a stock level that produces maximum sustainable yield (MSY). The paucity of biological and fisheries information for many stocks has led to identifying surrogate RPs for the fishing mortality (F_{MSY}) and stock biomass level (B_{MSY}) that produce MSY. Although most of these surrogate RPs are derived for finfish stocks from an age-based analysis (Clark 1993), a number of them have been either directly applied or estimated for crab stocks. Some F_{MSY} proxies used in or estimated for crab stock management are natural mortality (M) for Bering Sea crab stocks (North Pacific Fishery Management Council (NPFMC) 1999) and $F_{0.1}$ used for Bering Sea crab stocks in the early 1990s (Reeves 1994) and proposed for Canadian Dungeness crab (*Cancer magister*) stocks (Zhang et al. 2002).

Traditional age-based population models, which mostly assume continuous growth, are not directly applicable to crab stocks because growth is discontinuous and routine ageing techniques are lacking even though lipofuscin age markers have recently been used to age blue crab (*Callinectes sapidus*) (Ju et al. 2003). Size-based population models (e.g., Zheng et al. 1995; Miller 2001) have been developed for crab stocks, but the suitability of F_{MSY}-based RPs for crab stocks has not been investigated fully using size-based analyses. High-latitude crab stocks, which are the focus of this paper, pose additional problems in assessment because most of them are managed by a males-only exploitation strategy, which is capable of drastically changing the sex ratio and possibly reducing the reproductive potential (Smith and Jamieson 1991; Rondeau and Sainte-Marie 2001); additionally, fishery information on the female component of these stocks is not available for comprehensive assessment.

In this paper, we briefly review decision rules currently used in the management of two major high-latitude crab fisheries in the United States and Canada and then contrast these present systems against the results of a size-based RP estimation procedure that incorporates crab life history parameters, including reproductive characteristics and recruitment variability. The analysis will also evaluate the RP decision rules against variation in the size, sex, and season rules that presently exist in these fisheries. The RP estimator is robust for data-poor and data-rich situations. The RPs can be used with or without actual survey biomass estimates for management purposes. Finally, we use the RP estimator to determine various RPs for relatively data-rich Bering Sea and eastern Canada snow crab (*Chionoecetes opilio*) stocks and data-poor Southeast Alaska and western Canada Dungeness crab stocks for referential system comparison.

Review of RPs in selected high-latitude crab fisheries in the United States and Canada

United States

Federally managed fisheries in the United States exclusive economic zone are directed by the Magnuson–Stevens Fishery Conservation and Management Act to manage in a precautionary fashion to attain near MSY-producing stock and exploitation levels on a long-term basis. The stock status determination criteria are definitions of overfishing (on F scale) and overfished conditions (on B scale) intended for use by the councils and US government to monitor the stock condition. If F exceeds the overfishing level, then the stock is declared to be subject to overfishing, and if the stock declines below the overfished biomass level, then the stock is declared overfished, and management actions in the form of reducing F or rebuilding plans must be implemented (Restrepo and Powers 1999).

The United States federal government through the NPFMC and the State of Alaska jointly manages the Bering Sea and Aleutian Islands crab stocks, whereas the State of Alaska solely manages the Gulf of Alaska and Southeast Alaska crab stocks. For the Bering Sea and Aleutian Islands crab stocks, the NPFMC (1999) defined the "overfishing" level by a constant fishing mortality MSY-Control Rule equating F_{MSY} to M. Because of the lack of plausible M estimates for each crab stock, an M of 0.3 for the *Chionoecetes* species group has been adopted. The M estimate was derived using Hoenig's (1983) formula relating M to longevity. The NPFMC defined the "overfished" status by the minimum stock size threshold, which is equal to half of the MSY stock size. The MSY stock size is estimated as the average total mature stock biomass observed over the 15-year period from 1983 to 1997, which is regarded as ecologically stable (NPFMC 1999).

In addition to federal management regulations, the Alaska Department of Fish and Game (ADFG) has developed harvest strategies for *Chionoecetes* species crab stocks in selected fisheries of the Bering Sea and Gulf of Alaska. The harvest strategies aim at keeping sufficient spawning biomass for stock productivity by controlling the removal of mature males. Guideline harvest level (GHL) is determined for the exploitable portion of a stock based on a stock abundance estimate and a target harvest rate, and minimum (threshold) stock size level (mainly of mature portion) and minimum GHL (for a few stocks) are also estimated for assessing stock viability and manageability under continued fishing. The Bering Sea and Aleutian Islands snow crab fishery is managed by sex (males only), size, and season restrictions with a GHL determined from mature male abundance. In addition, fishery performance within a season is monitored, and if the fishery is expected to exceed the GHL before the declared closure date, then the season is ended by an ADFG Commissioner's emergency order. Single-sex harvest has been in effect since the late 1940s to protect mature females for reproduction. Specific fishing seasons are set to avoid harvesting crabs during mating and molting (soft-shell) periods. To avoid overharvest of legal males within the GHL, a maximum harvest of 60% of the estimated abundance of exploitable legal males is enforced (Pengilly and

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Schmidt 1995). Incidental mortality of crabs in other fisheries (trawl, pot, and dredge) is reduced by enforcing maximum allowable crab bycatch thresholds, which are calculated as a percentage (of the crab abundance) in those fisheries, and closed areas (NPFMC 2001).

Because the stock assessment program for Southeast Alaska Dungeness crab stocks is in its infancy and population parameters are not well described, current management is primarily passive. The ADFG regulations for this fishery include a minimum size, males-only fishery, and a season closure during the late-summer female molting and mating period (16 August – 30 September) and for part of the male molting period (1 March – 14 June). However, the summer season significantly overlaps the late-spring and early-summer end of the primary male molting period (Koeneman 1985), and handling of soft-shelled crabs during the summer season can be extremely high in some years and areas (ADFG 2002). Southeast Alaska Dungeness crab management is based on the concept that if a single age-class of functionally mature prerecruit males are allowed to participate in mating prior to recruiting into the fishery, then virtually all legal males may be removed annually if crabs are protected during their mating and molting period. Harvest rates are roughly estimated to exceed 85% in some years. Nonetheless, when effort began increasing in the late 1980s, a complex system of limited entry, with four different pot number tier levels and a maximum number of entrants and pots, was implemented in 1997 (Shirley 1993). There are no GHLs set for this fishery and harvests are extremely variable between years, generally ranging from 900 to 2300 t depending on the strength of recruitment (ADFG 2002). Currently, year-class strength is assessed from the catch rate at the beginning of the fishery and there is allowance for curtailing fishing if a catastrophic year-class failure is detected. A stock assessment pot survey and tagging program is under development with goals of better describing life history parameters and providing a preseason index of crab abundance. Although only seven fishing districts are currently surveyed, approximately 70% of the annual harvest occurs in the surveyed districts.

Canada

Every Canadian snow crab stock is managed by sex (males only), size, season, effort (limited number of participants and traps by participant), and quota (total allowable catch and individual transferable quota). A consensus opinion has emerged that males have a terminal molt to maturity and this has important implications for management (Conan and Comeau 1986; Sainte-Marie et al. 1995). Discarding of legal-size males is in principle prohibited everywhere to prevent high-grading by shell condition or size, which can result in resource wastage and reduced yield per recruit. However, for some stocks, careful discarding of legal-size adolescent (preterminal molt) males and of soft-shelled adult males is encouraged as a measure to maximize yield per recruit and increase the probability of males mating at least once (Dufour et al. 1997; Bourassa and Dufour 2000). To limit handling mortality, partial or complete closures are imposed for some stocks when the proportion of soft-shelled crabs present in at-sea samples remains above 20% for a threshold number of consecutive days. Comprehensive, fishery-independent trawl or trap surveys exist for most stocks (e.g., Loch et al. 1995) and they provide information on both sexes (trawl) or mainly on males (trap). However, no analytically based RPs have been developed, and management of stocks currently depends on trends in survey biomass and age structure (from proxy shell condition), indices for prerecruits and recruits, fishery performance evaluation, and, in some places, monitoring of female reproductive condition.

The Dungeness crab fishery in Canada occurs in the waters off British Columbia. The coastal fisheries are divided into seven management areas. These areas vary from large physical regions such as the open-ocean fishery in Hecate Straits to small isolated inshore fisheries in the central coast fiords. The commercial fishery is managed by size and sex (males only) restrictions in all regions of the coast. The sport and First Nations fisheries are restricted by size alone. Additional management measures are implemented for the commercial fishery in specific regions of the coast depending on the biological, social, and economic objectives set for the specific area. These restrictions may include specific seasons to avoid handling mortality issues such as soft-shell periods. Exploitation rates in many areas of the coast are estimated to be well in excess of 0.9. The assessment of the fisheries to date has been to provide advice on ways to reduce mortality on sublegal male or female crabs. In general, there is a lack of biological information from most of the management regions, although there have been advisory documents suggesting the need to restrict the effort in certain fisheries. Recent directed studies of a fished and unfished population in close proximity have resulted in ongoing discussions and recommendations for adopting control rules based on $F_{0.1}$ on legal crabs and (or) fishery performance data indicating unacceptably high rates of discard crabs in the catch (Zhang et al. 2002).

RP estimation procedure

Siddeek (2003*a*) developed a size-based method to estimate RPs for Bristol Bay red king crab (*Paralithodes camtschaticus*) that incorporated size-invariant mortality and deterministic stock–recruitment (S–R) relationships. In this paper, that procedure was extended to incorporate size- and sex-specific mortality, complex mating behavior, and stochastic S–R relationships to determine the same set of RPs for the United States and Canada snow and Dungeness crab stocks. The RPs included threshold values of harvest rate, $U(F_{MSY})$, effective spawning biomass ratio, $ESB(F_{MSY})/ESB(0)$, and nominal mature biomass ratio, $SSB(F_{MSY})/SSB(0)$. The $U(F_{MSY})$ was considered as an F-based threshold (a limit RP), the $ESB(F)$ was used in an S–R relationship to generate recruits, the $SSB(F_{MSY})/SSB(0)$ was treated as a B-based threshold (a limit RP), and the $ESB(F_{MSY})/ESB(0)$ was considered as another form of a B-based threshold (a limit RP).

Methods and materials

The notation used in the text, tables, and appendices are defined in the list of notations immediately after the list of references.

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Determination of F_{MSY}, $U(F_{MSY})$, ESB(F_{MSY})/ESB(0), and SSB(F_{MSY})/SSB(0)

Determination of F_{MSY}-based RPs requires an S–R relationship, which is a difficult task for many stocks. Two well-known S–R models, Beverton–Holt (Beverton and Holt 1957) and Ricker (1954), with a plausible range of S–R shape parameter (τ) were used to explore the patterns and trends in RPs. To estimate RPs, first, initial cohort (prerecruit-1 and class-1) abundance was generated under a Beverton–Holt or Ricker S–R model using a set of formulas based on spawning biomass per recruit (Mace 1994). Second, a threshold fishing mortality was determined by maximizing the legal male yield for a given set of growth, fishery selectivity, and other mortality parameters (natural mortality, sublegal crab handling mortality, and bycatch mortality) for the deterministic S–R model. Third, the recruitment was randomly varied to generate a 100-generation fishery and the average legal male yield over 100 generations was maximized in a similar way to obtain another threshold fishing mortality. Although the latter threshold fishing mortality was closer to F_{MSY}, both estimates were treated as F_{MSY} because the central values of harvest rates under deterministic and stochastic recruit generations were the same (see the Results section). The F_{MSY} was determined by systematically searching for a maximum $Y(F)$ over the effective F (annual $F \times$ fishing period) within 0.0–5.0 by a small step of 0.1. The $U(F_{MSY})$ was estimated by dividing the MSY catch by the average MSY standing stock size of legal crabs. The effective spawning biomass based on plausible mating ratio and nominal mature biomass that ignored the mating ratio was also determined at F_{MSY}. The SSB(F_{MSY})/SSB(0) at F_{MSY} corresponds to the proportion of virgin biomass (so called "B-based RP"; Williams and Shertzer 2003) in the traditional $F_{@SSB(\%)}$ that maintains the mature biomass at the MSY-producing level. Mace (1994) followed a deterministic approach to generate the number of recruits. We incorporated recruitment variation in the S–R models to determine RP distributions. We considered separately female and combined sexes spawning biomass per recruit for recruit generation from S–R models. A flowchart showing the steps to estimate RPs is given in Fig. 1 and the spawning biomass per recruit derivation formulas are explained in Appendix A with underlying assumptions. Published and plausible biological and fisheries information on snow and Dungeness crab stocks that were used in the simulations are also provided (Appendix B).

Recruitment was modeled using the following two S–R models (Beverton and Holt (1957) and Ricker (1954), respectively) with lognormal random errors:

$$(1) \qquad R_t = \frac{\mathrm{ESB}}{\alpha + \beta \mathrm{ESB}} e^{\varepsilon_t - \sigma_\varepsilon^2/2}$$

and

$$(2) \qquad R_t = \gamma \mathrm{ESB} e^{-\theta \mathrm{ESB}} e^{\varepsilon_t - \sigma_\varepsilon^2/2}$$

where $\varepsilon_t = \rho\varepsilon_{t-1} + \epsilon_t$ and $\epsilon_t \sim N(0, \sigma_\epsilon^2)$ and ε_t is set to $Z\sigma_{\varepsilon_t}$ where $Z \sim N(0, 1)$ and

$$\sigma_{\varepsilon_t}^2 = \frac{\sigma_\epsilon^2}{1-\rho^2}$$

From the deterministic form of the S–R relationship, the R_{max} for the Beverton–Holt S–R relationship is $1/\beta$ and that for the Ricker S–R relationship is $\gamma e^{-1}/\theta$.

Following Mace (1994), the S–R shape parameter (in Mace's terms, the extinction parameter), τ, can be written as

$$(3) \qquad \tau = \frac{(\mathrm{ESB}/R)_{\mathrm{ESB}=0}}{(\mathrm{ESB}/R)_{F=0}}$$

where $(\mathrm{ESB}/R)_{\mathrm{ESB}=0}$ equals α for the Beverton–Holt S–R model and $1/\gamma$ for the Ricker S–R model. Therefore

$$(4) \qquad \alpha = \tau(\mathrm{ESB}/R)_{F=0}$$

for the Beverton–Holt S–R model and

$$(5) \qquad \gamma = \frac{1}{\tau(\mathrm{ESB}/R)_{F=0}}$$

for the Ricker S–R model.

Thus, for a given τ and a fixed R_{max}, all parameters of the S–R relationships can be determined from an estimate of $(\mathrm{ESB}/R)_{F=0}$. Furthermore, by varying the τ value, different steepness (near the origin) and shape of the S–R curve can be obtained.

For RP estimation, $R(F)$, ESB(F), SSB(F), and $Y(F)$ estimates for the two S–R models are needed (Appendix A). The $R(F)$ was determined using the following formulas (Beverton and Holt (1957) and Ricker (1954), respectively) with either $(\mathrm{ESB}_{\mathrm{female}}/R)_F$ or $(\mathrm{ESB}_{\mathrm{combined\ sexes}}/R)_F$ determined from Appendix A formulas:

$$(6) \qquad R(F) = \frac{(\mathrm{ESB}/R)_F - \alpha}{\beta(\mathrm{ESB}/R)_F}$$

$$(7) \qquad R(F) = \frac{\ln(\gamma(\mathrm{ESB}/R)_F)}{\theta(\mathrm{ESB}/R)_F}$$

The M, h, BYM, and mating ratios involved in RP estimation were plausible fixed values selected from either literature or unpublished information (Appendix B). On the other hand, the τ value is largely unknown because of a lack of S–R relationship for many crab stocks (Zheng and Kruse 2003), and hence, a uniform distribution with a plausible continuous range was used to select the τ parameter.

Two types of simulations were performed to explore RPs. First, recruits were estimated from the deterministic form of the two S–R models for 500 randomly selected τ values from a uniform distribution in the 0.20–0.50 interval, and mean, median, and standard deviation of RPs were determined. Second, the estimated recruits were perturbed to simulate a 100-generation fishing history at different F levels, and mean yield at each F was determined from which the F_{MSY} and related RPs were calculated. Then the 2.5 and 97.5 percentiles, mean, median, and standard deviation of RPs were estimated. This simulation procedure can be explained by the following steps. (1) A set of 100 standard normal random numbers were used to perturb a set of 100 recruitments generated by spawning biomasses resulting from 100 generations of fishing (i.e., the simulation was dynamic with each perturbed recruitment producing different subsequent biomass), starting from a virgin stock, at a fixed F for fixed values of σ_ϵ^2 and ρ and a randomly selected value of τ, and an average (sustainable) yield at each F value was calculated. (2) The

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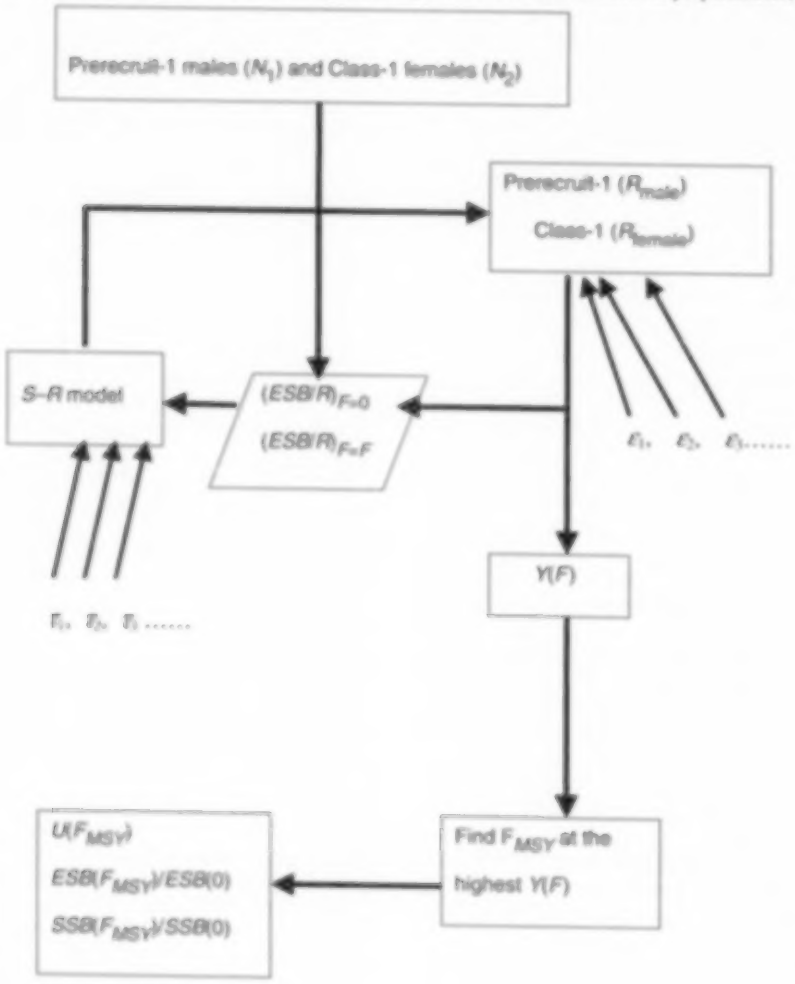
Fig. 1. Flow chart showing the approach to reference point estimation. $(ESB/R)_{F=F}$ and $(ESB/R)_{F=0}$, effective spawning stock biomass per recruit corresponding to a fishing mortality F and $F = 0$, respectively; $U(F_{MSY})$, exploitation rate corresponding to MSY-level fishing mortality F_{MSY}; ESB(F), ESB(F_{MSY}), and ESB(0), effective spawning stock biomass corresponding to a fishing mortality F, F_{MSY}, and $F = 0$, respectively; SSB(F), SSB(F_{MSY}), and SSB(0), nominal total mature stock biomass corresponding to a fishing mortality F, F_{MSY}, and $F = 0$, respectively; $Y(F)$, total yield for a fishing mortality F; τ, stock–recruitment shape parameter; ε, random error term.



F_{MSY} and related RPs were determined by searching for the F that produced the maximum average yield. (3) Steps 1 and 2 were then repeated for 500 τ values to obtain 500 RP values from which mean, median, and standard deviation of all RPs and a frequency distribution of one of the RPs, the harvest rate, were generated. In the first type of simulation, mean and median RPs were estimated for various scenarios of M, h, initial sex ratio, minimum legal size, fishing period, molting to fishing period, and type of spawner participant (female or combined sexes). The first simulation was a sensitivity analysis on RPs. In the second type of simulation, mean and median RPs were determined for low and high values of σ_ε^2 and ρ with an arbitrarily selected single type of S–R model, spawner participant, and status quo values of other parameters. The purpose of the latter simulation was to explore the behavior of RPs under low and high recruitment perturbations and autocorrelation. Moreover, the latter simulation provides RPs related to long- term average yields, which correspond to the MSY yield defined in the US Magnuson–Stevens Fishery Conservation and Management Act. The autocorrelation scenario was considered only for the snow crab stocks because the Bering Sea and Canada snow crab recruitment dynamics appear to have this characteristic: low recruitment is followed by low recruitment and vice versa (Sainte-Marie et al. 1995; Comeau et al. 1998; Zheng and Kruse 2003). Information on the recruitment dynamics of Dungeness crab is lacking for both areas, and hence, the autocorrelation factor was ignored in the simulations. Simulations were performed with Fortran 90 with International Mathematical and Statistical Library (2000)

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routines for standard normal (RNNOA) and uniform (RNUN) random number generations using a fixed initial seed value.

Snow crab input values and RP estimation procedure

Bering Sea stock

The effective minimum size of retained crab, 102 mm carapace width (CW), is due to industry preference even though the ADFG prescribed a lower minimum legal size, 78 mm CW. Mature crabs of both sexes were assumed to have a terminal molt (Turnock 2003). We explored the effects on RPs of changes in the minimum capture size by ±10 mm CW. The purpose of this exercise was to investigate whether harvest rate could be increased (or decreased) with an increase (or decrease) in minimum size at first capture without jeopardizing the spawning potential. Small mature males may be capable of effectively inseminating fewer females than larger males during a breeding season owing to smaller gonads (Rondeau and Sainte-Marie 2001; B. Sainte-Marie, unpublished data). Therefore, plausible male to female mating ratios of 1:4 and 1:3 were selected for mature males <95 mm CW for primiparous and multiparous females, respectively (Appendix B, Table B2). For mature males ≥95 mm CW, the respective ratios were 1:9 and 1:6. Newly molted mature males are not expected to mate with mature females (Conan and Comeau 1986). So, new-shell, mature, male crab abundances were disregarded in calculating the effective spawning biomass. A conservative M value of 0.30 was used for both sexes (NPFMC 1999). The instantaneous handling mortality, $HM1_y$, was related to F through the selectivity function and handling mortality rate h. There was a 25% handling mortality rate ($h = 0.25$) on captured and subsequently released sublegal male and female crabs (Zheng et al. 2002). An h value of 0.25 was selected. Zero and 50% handling death rates were also considered in the RP simulations. The BYM was fixed at 0.01, which represents an estimate of maximum BYM based on 1994–1999 bycatch weighted (by stock size) average harvest rates from all nondirected fisheries (Siddeek 2002).

In general, the fishing season starts in mid-January and lasts until the GHL is achieved. The mean estimate of δ for the 1995–2002 fishing seasons was 0.1303 year (Siddeek 2003*b*). There is no precise identification of molting period for the Bering Sea snow crabs. The molting period may extend from February to July or early August with possible peaks in March, May, or June (R.S. Otto and B.G. Stevens, National Marine Fisheries Service, 301 Research Court, Kodiak, AK 99615, USA, personal communication). An arbitrary T value of 0.6667 (lapsed time between the midmolting period on 15 May and the fishery start date on 15 January) was used in the simulation for status quo RP determination. A zero T value was also considered to explore its effect on RPs.

The initial male to female ratio was set at 1:2 and the simulations were started with a maximum recruit number of 1000 for females and 500 for males. The number of males entering the prerecruit-1 size group (82–101 mm CW) was likely to be closer to half of the females entering the class-1 size group (50–59 mm CW) because of the possibility of male terminal molt occurring at sizes <82 mm CW (Sainte-Marie et al. 1995). The subsequent number of progenies produced by the spawners (i.e., total prerecruit-1 and class-1 crabs) was divided into 1:2 between new-shell prerecruit-1 males and new-shell class-1 females and distributed within each 5-mm interval in the respective stage using a normal distribution with mean equal to the midvalue of the size range and standard deviation approximately equal to the stage size range divided by 6. The initial male to female ratio was also changed to 3:4 to explore its effect on RPs. The subsequent growth increment at each molt was assumed to be normally distributed with size-specific means and standard deviations to determine proportion (P_{ij}) of crabs falling into each size bin as a result of growth. Plausible prerecruit-1 age of 6 years for males, class-1 age of 4 years for females (Somerton 1981; Reeves 1994), and a maximum age of 16 years (based on 1% survival at the maximum age for an M of 0.30) were used to track the cohort for RP estimation.

Eastern Canada stock

The estimation procedures were the same as that for the Bering Sea stock with a few exceptions, but the input parameter values differed and were derived when available from stocks in the estuary and northern Gulf of St. Lawrence. All mature females and males were considered to be terminally molted individuals. The total catch was estimated only for the mature postmolt 2- to 4-year age groups. The minimum legal size is 95 mm CW. So, we explored the effects on RPs for changes in the minimum capture size by ±10 mm CW. The selection of mating ratio was the same as before, but different M values were used for different postmolt ages and sexes (Appendix B, Table B2). An h value of 0.12 and a BYM value of 0.01 were considered in RP simulations. Zero and 25% handling mortality rates were also considered.

The spring fishery in the estuary and northern Gulf of St. Lawrence starts in April and the catch quotas are usually met within about 10 weeks. Thus, the estimate of δ was 0.1923 year. The peak molting period is May; therefore, a T value of 0.875 (lapsed time between the midmolting period on 15 May and the fishery start date on 1 April) was used in the simulation for status quo RP determination. A zero T value was also considered for RP calculation.

The number of individuals entering the cohort, the initial male to female ratio, and the initial size frequency distribution were set the same as for the Bering Sea stock. However, the size-classes used in the model were different from those used for the Bering Sea stock. Plausible prerecruit-1 and class-1 ages (approximately 7.5 years for males and 5.5 years for females) and maximum ages (approximately 18.0 years for males and 13.0 years for females) (Sainte-Marie et al. 1995; Alunno-Bruscia and Sainte-Marie 1998) were used to track the cohort for RP estimation.

Dungeness crab input values and RP estimation procedure

Southeast Alaska stock

The same estimation procedures used for snow crab analyses were applied to Dungeness crab stocks, but the input parameter values differed. The minimum legal size is 165 mm CW. We explored the effects on RPs for changes in the minimum capture size by ±10 mm CW. Because infor-

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mation on mating ratio is lacking for the Dungeness crab stocks, an arbitrary mating ratio of 1:3 borrowed from other families of crabs (Siddeek 2002, 2003*a*, 2003*b*) was used for the entire mature size groups. An M value of 0.47 (G. Bishop, unpublished data), an h value of 0.15, and a BYM value of 0.01 were chosen for RP estimation (Appendix B, Table B3). Zero and 30% handling mortality rates were also considered in the analyses.

The Southeast Alaska summer fishery starts on 15 June and ends on 15 August and the fall and winter season fishery starts on 1 October, ending 30 November or 28 February, depending on location. The fishery is 4 or 5 months in duration depending on the major fishing area. Based on the 4-month duration, the estimate of δ was 0.3333 year. The molting period extends from spring to summer and an arbitrary peak molting date of 15 April was considered for estimating T, which was 0.4583 year. A *zero* T value was also considered for RP determination.

The initial male to female ratio was set at 1:1, and the simulations were started with a maximum recruit number of 1000 for each sex. The subsequent number of progenies produced by the spawners was divided into 1:1 between new-shell prerecruit-1 males and new-shell class-1 females and distributed within each 5-mm interval following the same procedure used for snow crab. Plausible prerecruit-1 age of 3 years for males, class-1 age of 1 year for females (based on Butler's (1961) age-specific size data), and a maximum age of 10 years (based on 1% survival at the maximum age for an M of 0.47) were used to follow the cohort life span for RP determination.

Western Canada stock

The estimation procedures were the same as those for the Southeast Alaska stock with a few changes in the input parameter values (Butler 1961; Smith and Jamieson 1989). The minimum legal size is 155 mm CW (note: CW in this case refers to notch-to-notch measurement that is equivalent to the legal size limit of 165 mm as measured point-to-point). We explored the effects on RPs for changes in the minimum capture size by ±10 mm CW. The selection of mating ratio was the same as that for the Southeast Alaska stock. However, the M values were much higher; an M value of 0.91 for the prerecruit-1 males and class-1 females and another M value of 0.75 for the recruits and postrecruit males and class-2 females (Z. Zhang and J. Boutillier, unpublished data). The selection of h and BYM was the same as that for the Southeast Alaska stock.

The Fraser River Delta fishery on the western coast of Canada is from 1 July to 30 November, which provided a δ value of 0.4167 year. Considering an approximate peak molting time of 1 May, the T value was estimated at 0.1667 year. A *zero* T value was also considered for RP estimation.

The initial number of individuals entering the cohort and the initial male to female ratio were set the same as for the Alaska stock. Plausible prerecruit-1 age of 2 years for males, class-1 age of 1 year for females (based on Butler's (1961) age-specific size data), and a maximum age of 6 years (based on 1% survival at the maximum age for an M of 0.83 (mean of 0.91 and 0.75)) were used to follow the cohort life span for RP determination.

Results

Comparison of snow crab RPs

We compared the RP estimates for each stock for different input parameter values, between stocks of the same species for respective status quo input parameter values, and for each stock for variability of RPs under recruitment variation for the status quo input parameter values. The effects on RPs for changes in input parameter values were similar for the deterministic Beverton–Holt and Ricker S–R models. For brevity, we provided most results for the Beverton–Holt S–R relationship, which produced a lower harvest rate than the Ricker S–R model.

Bering Sea stock

The mean harvest rate under a deterministic Beverton–Holt S–R relationship increased from 0.31 to 0.36 as the minimum legal size was increased from 92 to 112 mm CW for the combined sexes spawners. At the current minimum marketable size of 102 mm CW, the mean harvest rate (±SD) was 0.37 (±0.04) and the mean SSB(F_{MSY})/SSB(0) ratio was 0.48 (±0.02). When only females were considered as spawners, the mean harvest rate at the current minimum marketable size increased to 0.49 (±0.05). As the handling mortality was increased, the mean harvest rate decreased slightly, but when it was reduced to *zero*, the mean harvest rate increased dramatically to 0.50 and the mean SSB(F_{MSY})/SSB(0) ratio also increased to 0.54. There were very small changes in the mean SSB(F_{MSY})/SSB(0) ratio for these scenarios (0.43–0.48) except for the *zero* handling mortality rate. Changing the current fishery opening date in relation to the peak molting time did not affect any of the RPs. Halving or doubling the current fishing period also did not affect the mean RP values. On the other hand, the change in the initial male to female ratio from 1:2 to 3:4 increased the mean harvest rate from 0.37 to 0.43 and reduced the mean ESB(F_{MSY})/ESB(0) ratio from 0.55 to 0.53 and the mean SSB(F_{MSY})/SSB(0) ratio from 0.48 to 0.43. There were very small differences among the mean and median values of all RPs (Table 1).

Eastern Canada stock

The eastern Canada stock exhibited RP trends similar to those of the Bering Sea stock but with slightly higher harvest rates. The mean harvest rate under a deterministic Beverton–Holt S–R relationship increased from 0.32 to 0.40 as the minimum capture size was increased from 85 to 105 mm CW for the combined sexes spawners. At the current minimum legal size of 95 mm CW, the mean harvest rate was 0.40 (±0.08) and the mean SSB(F_{MSY})/SSB(0) ratio was 0.49 (±0.02). When only females were considered as spawners, the mean harvest rate at the current minimum legal size increased to 0.44 (±0.05). There were very small changes in the mean SSB(F_{MSY})/SSB(0) ratio for these scenarios (0.49–0.50). The RPs behaved similarly to those of the Bering Sea stock for similar changes in start date of fishing from the molting period, fishing period, handling mortality, and initial male to female ratio. There were very little differences among the mean and median values of all RPs (Table 2).

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Table 1. Comparison of reference point estimates (mean, median) for Bering Sea snow crab for various scenarios for 500 randomly selected S–R shape parameter (τ) values within 0.20–0.50, a BYM of 0.01, an M of 0.30, under terminal molt of mature components of both sexes assumption, and recruits deterministically generated from the Beverton–Holt S–R model.

Spawners	Total	Total	Total	**Female**	Total	Total	Total	Total	Total	Total
Initial male:female ratio	1:2	1:2	1:2	1:2	1:2	1:2	1:2	**3:4**	1:2	1:2
L_v (mm CW)	**92**	102	**112**	102	102	102	102	102	102	102
T	0.6667	0.6667	0.6667	0.6667	**0.0000**	0.6667	0.6667	0.6667	0.6667	0.6667
δ	0.1303	0.1303	0.1303	0.1303	0.1303	0.1303	0.1303	0.1303	**0.2606**	**0.0652**
h	0.25	0.25	0.25	0.25	0.25	**0.00**	**50.00**	25.00	0.25	0.25
$U(F_{MSY})$	0.31, 0.29 (0.04)	0.37, 0.34 (0.04)	0.36, 0.34 (0.05)	0.40, 0.39 (0.05)	0.37, 0.34 (0.04)	0.50, 0.50 (0.07)	0.32, 0.32 (0.03)	0.43, 0.42 (0.05)	0.36, 0.34 (0.04)	0.37, 0.35 (0.04)
$ESB(F_{MSY})/ESB(0)$	0.51, 0.52 (0.02)	0.55, 0.55 (0.02)	0.57, 0.57 (0.02)	0.54, 0.54 (0.01)	0.55, 0.55 (0.02)	0.62, 0.62 (0.01)	0.48, 0.48 (0.03)	0.53, 0.52 (0.02)	0.55, 0.55 (0.02)	0.55, 0.55 (0.02)
$SSB(F_{MSY})/SSB(0)$	0.45, 0.46 (0.02)	0.48, 0.48 (0.02)	0.49, 0.49 (0.01)	0.48, 0.47 (0.01)	0.48, 0.48 (0.02)	0.54, 0.54 (0.01)	0.43, 0.43 (0.03)	0.43, 43 (0.01)	0.48, 0.48 (0.02)	0.48, 0.48 (0.02)

Note: Total is combined sexes, and other parameters are defined in the notation section. Values and text in bold refer to changes in input values, and values in parentheses are standard deviations.

Table 2. Comparison of reference point estimates (mean, median) for eastern Canada snow crab for various scenarios for 500 randomly selected S–R shape parameter (τ) values within 0.20–0.50, a BYM of 0.01, variable M values, terminal molt of mature components of both sexes, and recruits deterministically generated from the Beverton–Holt S–R model.

Spawners	Total	Total	Total	**Female**	Total	Total	Total	Total	Total	Total
Initial male:female ratio	1:2	1:2	1:2	1:2	1:2	1:2	1:2	**3:4**	1:2	1:2
L_v (mm CW)	**85**	95	**105**	95	95	95	95	95	95	95
T	0.875	0.875	0.875	0.875	**0.000**	0.875	0.875	0.875	0.875	0.6667
δ	0.1923	0.1923	0.1923	0.1923	0.1923	0.1923	0.1923	0.1923	**0.3846**	**0.0962**
h	0.12	0.12	0.12	0.12	0.12	**0.00**	**0.25**	0.12	0.12	0.12
$U(F_{MSY})$	0.32, 0.31 (0.04)	0.40, 0.40 (0.08)	0.40, 0.40 (0.06)	0.44, 0.45 (0.05)	0.40, 0.40 (0.08)	0.45, 0.45 (0.07)	0.33, 0.35 (0.06)	0.51, 0.53 (0.02)	0.35, 0.34 (0.05)	0.36, 0.35 (0.05)
$ESB(F_{MSY})/ESB(0)$	0.49, 0.49 (0.03)	0.49, 0.48 (0.04)	0.48, 0.48 (0.03)	0.48, 0.48 (0.02)	0.49, 0.48 (0.04)	0.48, 0.47 (0.03)	0.50, 0.49 (0.05)	0.72, 0.72 (0.01)	0.50, 0.50 (0.03)	0.50, 0.50 (0.03)
$SSB(F_{MSY})/SSB(0)$	0.50, 0.50 (0.02)	0.49, 0.49 (0.02)	0.49, 0.49 (0.02)	0.50, 0.50 (0.01)	0.50, 0.49 (0.02)	0.48, 0.47 (0.02)	0.51, 0.50 (0.03)	0.51, 0.51 (0.01)	0.50, 0.50 (0.02)	0.50, 0.50 (0.02)

Note: Total is combined sexes, and other parameters are defined in the notation section. Values and text in bold refer to changes in input values, and values in parentheses are standard deviations.

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Comparison of RPs between Bering Sea and eastern Canada stocks

The mean harvest rates for the Bering Sea stock were slightly lower than those for the eastern Canada stock under deterministic Beverton–Holt (0.37 versus 0.40) and Ricker S–R relationships (0.43 versus 0.48) and the mean nominal mature biomass ratios were also slightly lower under the respective S–R relationships (0.48 versus 0.49 and 0.53 versus 0.56, respectively). But the mean effective spawning biomass ratio behaved oppositely. The effects on threshold median RPs were similar (Tables 1–3).

We report only the 100-generation fishery simulations with the stochastic recruitment to the Beverton–Holt S–R model for brevity. The trends were the same for the Ricker model, but the harvest rates were higher. For the Bering Sea stock, the 2.5–97.5 percentile interval of harvest rate was 0.32–0.45 with a mean of 0.37 (±0.04) and a median of 0.34 for both low (0.7 and 0.6) and high (0.9 and 0.9) sets of σ_ε and ρ values and combined sexes spawners. The corresponding values for the eastern Canada stock were 0.29–0.53 with a mean of 0.40 (±0.08) and a median of 0.40. Thus, the amount of recruitment variability did not affect the central values of harvest rate within each stock, but the estimates for the eastern Canada stock were slightly higher because of different mortality and growth parameter values. The percentile limits for the nominal mature biomass ratios were similar for both stocks, 0.53–0.56 and 0.55–0.58 for the low- and 0.52–0.53 and 0.53–0.54 for the high-recruitment variability for the Bering Sea and eastern Canada stocks, respectively. The mean and median values for both stocks ranged 0.53–0.56 for the two levels of variability (Table 4). Thus, the MSY-level mature biomasses were slightly higher than half of the mature virgin biomass under the variable recruitment hypothesis. The distributions of harvest rate were skewed to the right for both stocks (Fig. 2). The distribution was truncated because the τ values were (randomly) selected from a fixed interval of 0.20–0.50. Individual results showed that the harvest rate was inversely related to τ. The mode toward the lowest harvest rate bin of the distribution indicated that at higher τ values, the RP estimator yielded closer harvest rate estimates. To estimate a realistic harvest rate value for a stock, a true τ value is needed, which can be calculated only if an S–R relationship is available for the stock.

We explored the RPs with the assumption of annual spawning. However, snow crabs may exhibit a 2-year reproductive cycle depending on environmental factors (Sainte-Marie 1993), especially temperature (Moriyasu and Lanteigne 1998). We examined the effect of this possibility on estimates of RP by halving the mating ratio of multiparous females. The mean harvest rate estimates for the deterministic Beverton–Holt S–R model were 0.37 versus 0.30 for the Bering Sea stock and 0.40 versus 0.33 for the eastern Canada stock under annual and biennial reproductive cycles, respectively. The corresponding median harvest rates were 0.34 versus 0.28 and 0.40 versus 0.29, respectively. The mean total mature biomass ratios were 0.48 versus 0.44 for the Bering Sea stock and 0.49 versus 0.44 for the eastern Canada stock under annual and biennial reproductive cycles, respectively. The corresponding median total mature biomass ratios were 0.48 versus 0.44 and 0.49 versus 0.45, respectively.

Table 3. Comparison of reference point estimates (mean, median) for Bering Sea and eastern Canada snow crab for 500 randomly selected S–R shape parameter (τ) values within 0.20–0.50, a BYM of 0.01, an initial male:female ratio of 1:2, and terminal molt of mature components of both sexes.

Stock	Bering Sea	Eastern Canada
L_∞ (mm CW)	102	95
T	0.6667	0.875
δ	0.1303	0.1923
h	0.25	0.12
M	0.30	Variable
$U(F_{MSY})$	0.43, 0.42 (0.08)	0.48, 0.45 (0.12)
$ESB(F_{MSY})/ESB(0)$	0.60, 0.60 (0.01)	0.52, 0.52 (0.02)
$SSB(F_{MSY})/SSB(0)$	0.53, 0.53 (0.01)	0.56, 0.56 (0.03)

Note: The recruits were simulated deterministically by the Ricker S–R model using combined sexes as spawners. Other parameters are defined in the notation section. Values in parentheses are standard deviations.

Comparison of Dungeness crab RPs

Southeast Alaska stock

The mean harvest rate under a deterministic Beverton–Holt S–R relationship increased from 0.79 to 0.93 as the minimum legal size was increased from 155 to 175 mm CW for the combined sexes spawners. At the current minimum legal size of 165 mm CW, the mean harvest rate was 0.79 (±0.09), the threshold median harvest rate was 0.79, and the mean nominal mature biomass ratio was 1.00 (±0.0001). When only females were considered as spawners, the mean and median harvest rates at the current minimum legal size increased to 0.96 (±0.0004). As the handling mortality was increased from 0.0 to 0.30, the mean and median harvest rates dropped from 0.93 to 0.64 and 0.63, respectively. Changes in T and fishing period had very little effect on any of the RP estimates. The mean and median nominal mature biomass ratios approached 1.00 for all scenarios except for zero handling mortality for which it was 0.41 (±0.01) (Table 5).

Western Canada stock

The western Canada stock exhibited RP trends similar to those of the Southeast Alaska stock under both S–R models but with slightly higher harvest rates and lower total biomass ratios owing to high M values and different growth parameter values. The mean harvest rate increased slightly from 0.85 to 0.88 as the minimum legal size was increased from 145 to 165 mm CW for the combined sexes spawners. The threshold median harvest rate increased from 0.83 to 0.87 for the same increase in legal size. At the current minimum legal size of 155 mm CW, the mean harvest rate was 0.85 (±0.03), the median harvest rate was 0.82, and the mean and median nominal mature biomass ratios were 0.92 (±0.01) and 0.91, respectively. When only females were considered as spawners, the mean and median harvest rates at the current minimum legal size increased to 0.88 (±0.04) and 0.87, respectively. The biomass ratios were over 0.90 and there were very little changes in the two biomass ratios except when handling mortality was zero. When handling mortality was zero, the mean and median harvest rates increased to

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Table 4. Comparison of 2.5–97.5 percentiles, mean, median, and standard deviation of reference point estimates for Bering Sea and eastern Canada snow crab for 500 randomly selected S–R shape parameter (τ) values within 0.20–0.50 and 100 perturbed recruits for 100-generation fishing at each F level.

Stock	Bering Sea	Bering Sea	Eastern Canada	Eastern Canada
L_∞ (mm CW)	102	102	95	95
T	0.6667	0.6667	0.875	0.875
ρ	0.60	0.90	0.60	0.90
σ_ε	0.70	0.90	0.70	0.90
δ	0.1303	0.1303	0.1923	0.1923
h	0.25	0.25	0.12	0.12
M	0.30	0.30	Variable	Variable
$U(F_{MSY})$				
2.5%–97.5%	0.32–0.45	0.32–0.45	0.29–0.53	0.29–0.53
Mean, median	0.37, 0.34	0.37, 0.34	0.40, 0.40	0.40, 0.40
SD	0.04	0.04	0.08	0.08
$ESB(F_{MSY})/ESB(0)$				
2.5%–97.5%	0.56–0.59	0.53–0.55	0.53–0.59	0.52–0.54
Mean, median	0.58, 0.59	0.54, 0.54	0.55, 0.55	0.53, 0.53
SD	0.01	0.003	0.02	0.01
$SSB(F_{MSY})/SSB(0)$				
2.5%–97.5%	0.53 – 0.56	0.52 – 0.53	0.55 – 0.58	0.53 – 0.54
Mean, median	0.55, 0.56	0.53, 0.53	0.56, 0.56	0.53, 0.53
SD	0.01	0.003	0.01	0.004

Note: The recruits were generated from the Beverton–Holt S–R model with combined sexes as spawners and an initial male:female ratio of 1:2. The reference points were determined by maximizing the average yield at each F level and mean and median reference point values were estimated for 500 S–R curves. The BYM was set at 0.01 and terminal molt of mature components of both sexes was assumed for both stocks. Other parameters are defined in the notation section.

Fig. 2. Distributions of harvest rate under 100-generation fishing for 500 randomly selected S–R shape parameter values under a stochastic Beverton–Holt S–R model. Histograms for (*a*) $\sigma_\varepsilon = 0.7$ and $\rho = 0.6$ and (*b*) $\sigma_\varepsilon = \rho = 0.9$ for the Bering Sea snow crab stock; histograms for (*c*) $\sigma_\varepsilon = 0.7$ and $\rho = 0.6$ and (*d*) $\sigma_\varepsilon = \rho = 0.9$ for the eastern Canada snow crab stock.

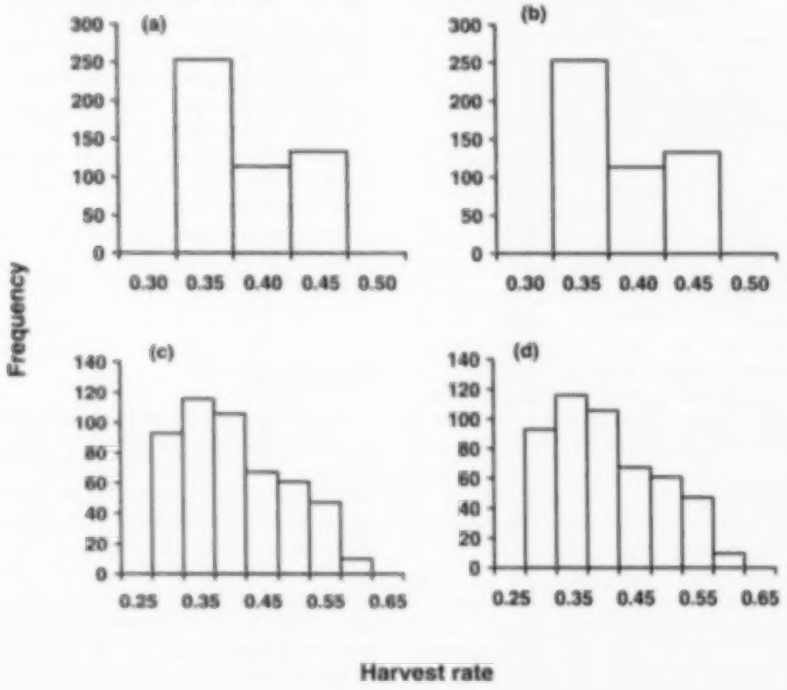

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Table 5. Comparison of reference point estimates (mean, median) for Southeast Alaska Dungeness crab for various scenarios for 500 randomly selected S–R shape parameter (τ) values within 0.20–0.50, a fixed BYM of 0.01, an M of 0.47 for both sexes, an initial male:female ratio of 1:1, and recruits deterministically generated from the Beverton–Holt S–R model.

Spawners	Total	Total	Total	Female	Total	Total	Total	Total	Total
L_c (mm CW)	**155**	165	**175**	165	165	165	165	165	165
$\bar{T}$	0.4583	0.4583	0.4583	0.4583	**0.0000**	0.4583	0.4583	0.4583	0.4583
$\bar{\delta}$	0.3333	0.3333	0.3333	0.3333	0.3333	0.3333	0.3333	**0.6666**	**0.1667**
h	0.15	0.15	0.15	0.15	0.15	**0.00**	**0.30**	0.15	0.15
U/F_{MSY}	0.79, 0.79	0.79, 0.79	0.93, 0.96	0.96, 0.96	0.79, 0.79	0.93, 0.93	0.64, 0.63	0.81, 0.80	0.79, 0.79
	(0.07)	(0.09)	(0.06)	(0.0004)	(0.09)	(0.002)	(0.06)	(0.11)	(0.08)
$ESB_0/F_{MSY}/ESB(0)$	1.00, 1.00	1.00, 1.00	1.00, 1.00	1.00, 1.00	1.00, 1.00	0.79, 0.79	1.00, 1.00	0.98, 1.00	1.00, 1.00
	(0.0001)	(0.0001)	(0.0001)	(0.0001)	(0.0001)	(0.03)	(0.0001)	(0.03)	(0.0001)
$SSB_0/F_{MSY}/SSB(0)$	1.00, 1.00	1.00, 1.00	1.00, 1.00	1.00, 1.00	1.00, 1.00	0.41, 0.41	1.00, 1.00	1.00, 1.00	1.00, 1.00
	(0.0001)	(0.0001)	(0.0001)	(0.0001)	(0.0001)	(0.01)	(0.0001)	(0.0001)	(0.0001)

Notes: Total is combined sexes, and other parameters are defined in the notation section. Values and text in bold refer to changes in input values, and values in parentheses are standard deviations.

0.94, while the mean and median total mature biomass ratios decreased to 0.51 and 0.52, respectively. The RPs behaved similarly to those of the Southeast Alaska stock for similar changes in $\bar{\delta}$, $\bar{T}$, and h (Table 6).

Comparison of RPs between Southeast Alaska and Western Canada stocks

The mean and median harvest rates under deterministic Beverton–Holt S–R relationship with combined sexes as spawners and status quo input parameter values were slightly higher for the western Canada stock (0.85 and 0.82, respectively) than those for the Southeast Alaska stock (0.79). The mean and median effective and total spawning biomass ratios were above 0.90 for both stocks (Tables 5 and 6). The central values of harvest rate under the deterministic Ricker S–R model behaved oppositely with Southeast Alaska stock estimates slightly higher than those for the western Canada stock (0.95–0.96 versus 0.93–0.94, respectively) (Table 7).

We restricted the 100-generation fishery simulations with the stochastic recruitment to the Beverton–Holt model for brevity. The trends were the same for the Ricker model, but the harvest rates were higher. For the Southeast Alaska stock, the 2.5–97.5 percentile interval of harvest rate was 0.66–0.92 with a mean of 0.79 (±0.09) and a median of 0.79 for both low (0.7) and high (0.9) σ_ε values, combined sexes spawners, and status quo other parameter values. The corresponding values for the western Canada stock were 0.82–0.90 with a mean of 0.85 (±0.03) and a median of 0.82 (Table 8). Thus, the amount of recruitment variability did not appreciably affect the harvest rate for this species either. The big difference in M between the two stocks did not have a dramatic effect on the harvest rate estimates, owing perhaps to different growth patterns dampening the effect of M on RP estimates for these stocks. The distribution of harvest rate was flat for the Southeast Alaska stock, while it was skewed to the right for the western Canada stock (Fig. 3). The reason for the truncated figures was previously explained. The flat distribution for the Southeast Alaska stock indicated that any harvest rate within that range was equally likely and the harvest rate estimate was strongly influenced by the τ value. This distribution pattern was unique to the Southeast Alaska stock. Other input parameters being similar, one possible reason for this pattern was different growth parameter values for this stock; the male growth increment was independent of the size, and the molt probability parameters were also quite different from those of the other stocks (see Appendix B).

Discussion

The threshold harvest rate was inversely related to the S–R shape parameter (τ) of the S–R curves. Since S–R relationships were lacking for the two crab species, τ values within a plausible range of 0.20–0.50 were used to explore the patterns and trends in RPs. The present τ range was wider on the lower side of τ values than that set for the Bristol Bay red king crab (Siddeek 2003*a*) to accommodate highly productive Dungeness crab. The Bristol Bay red king crab τ estimate of 0.24 (Siddeek 2003*c*) from an established S–R relationship (Zheng et al. 1995) justified this extension. Temporal and density variations in growth and maturity

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Table 6. Comparison of reference point estimates (mean, median) for western Canada Dungeness crab for various scenarios for 500 randomly selected S–R shape parameter (τ) values within 0.20–0.50, a fixed BYM of 0.01, a prerecruit-1 and class-1 M of 0.91, a recruit, postrecruit, and class-2 M of 0.75, an initial male:female ratio of 1:1, and recruits deterministically generated from the Beverton–Holt S–R model.

Spawners	Total	Total	Total	**Female**	Total	Total	Total	Total	Total
L_v (mm CW)	**145**	155	**165**	155	155	155	155	155	155
T	0.1667	0.1667	0.1667	0.1667	**0.0000**	0.1667	0.1667	0.1667	0.1667
δ	0.4167	0.4167	0.4167	0.4167	0.4167	0.4167	0.4167	**0.8334**	**0.2083**
h	0.15	0.15	0.15	0.15	0.15	**0.00**	**0.30**	0.15	0.15
$U(F_{MSY})$	0.85, 0.83	0.85, 0.82	0.88, 0.87	0.88, 0.87	0.84, 0.82	0.94, 0.94	0.75, 0.75	0.84, 0.88 (0.05)	0.87, 0.87 (0.01)
	(0.02)	(0.03)	(0.04)	(0.04)	(0.03)	(0.01)	(0.01)		
$ESB(F_{MSY})/ESB(0)$	1.00, 1.00	1.00, 1.00	1.00, 1.00	1.00, 1.00	1.00, 1.00	0.81, 0.81	1.00, 1.00	1.00, 1.00 (0.0001)	1.00, 1.00 (0.0001)
	(0.0001)	(0.0001)	(0.0001)	(0.0001)	(0.0001)	(0.03)	(0.0001)		
$SSB(F_{MSY})/SSB(0)$	0.93, 0.92	0.92, 0.91	0.97, 0.98	0.99, 1.00	0.92, 0.91	0.51, 0.52	0.91, 0.90	0.98, 1.00 (0.03)	0.88, 0.88 (0.03)
	(0.03)	(0.04)	(0.03)	(0.02)	(0.04)	(0.02)	(0.04)		

Note: Total is combined sexes, and other parameters are defined in the notation section. Values and text in bold refer to changes in input parameter values, and values in parentheses are standard deviations.

Table 7. Comparison of reference point estimates (mean, median) for Southeast Alaska and western Canada Dungeness crab for 500 randomly selected S–R shape parameter (τ) values within 0.20–0.50, a BYM of 0.01, an h of 0.15, and an initial male:female ratio of 1:1.

Stock	Southeast Alaska	Western Canada
Spawners	Total	Total
L_v (mm CW)	165	155
T	0.4583	0.1667
M	0.47	0.91, 0.75
$U(F_{MSY})$	0.95, 0.96 (0.02)	0.93, 0.94 (0.002)
$ESB(F_{MSY})/ESB(0)$	0.97, 0.96 (0.02)	1.00, 1.00 (0.0001)
$SSB(F_{MSY})/SSB(0)$	1.00, 1.00 (0.0001)	1.00, 1.00 (0.0001)

Note: The recruits were simulated deterministically by the Ricker S–R model. Total is combined sexes, and other parameters are defined in the notation section. Values in parentheses are standard deviations.

probability were ignored for simplicity in modeling. The simulations considered various random slope parameter values within this range and included both deterministic as well as stochastic recruitment to obtain central RP values. This assumes that there are many trajectories underlying a given S–R curve, perhaps owing to a given set of data covering different environmental regimes, and a central (mean and median) RP value within those trajectories was chosen as being representative. However, uncertainty in input parameter values compelled us to take a precautionary approach and suggest low harvest rate values from a harvest rate distribution. Since the distributions of harvest rate were mostly skewed, or flat in one case, median estimates were given with means. Random variation in recruitment was introduced into the model using overall low and high recruitment noises of 0.7 and 0.9 and, in the case of snow crab, an additional low and high autocorrelation parameter of 0.6 and 0.9. Similar low values of recruitment errors have been observed in some crab S–R model fittings (e.g., Bristol Bay red king crab; Zheng et al. 1995). The increase in S–R noise, however, did not affect the harvest rate estimates but changed the biomass ratio values.

The lower limits of size groups considered for RP determination were roughly 50% maturity size of males and females or above the 50% maturity size and approximately one molt increment below the legal size. We used these lower cutoff points with the expectation of using a constant M value among mature crabs in the simulations. However, a variable set of M values was used for the eastern Canada snow crab and western Canada Dungeness crab stocks because estimates of M were available for these stocks. By excluding mature males and females that are smaller than the lower size limit of prerecruit-1 or class-1 size groups, respectively, we have disregarded a portion of mature biomass in the S–R relationship. We assumed this to be minor in comparison with considering variable unknown M values at lower size groups. We also ignored the spatial distribution of different components of stocks in the model for simplicity. For example, only a portion of the total male breeding population may be available to mate either primiparous or multiparous snow crab females owing to depth segregation by age or size (Lovrich et al. 1995).

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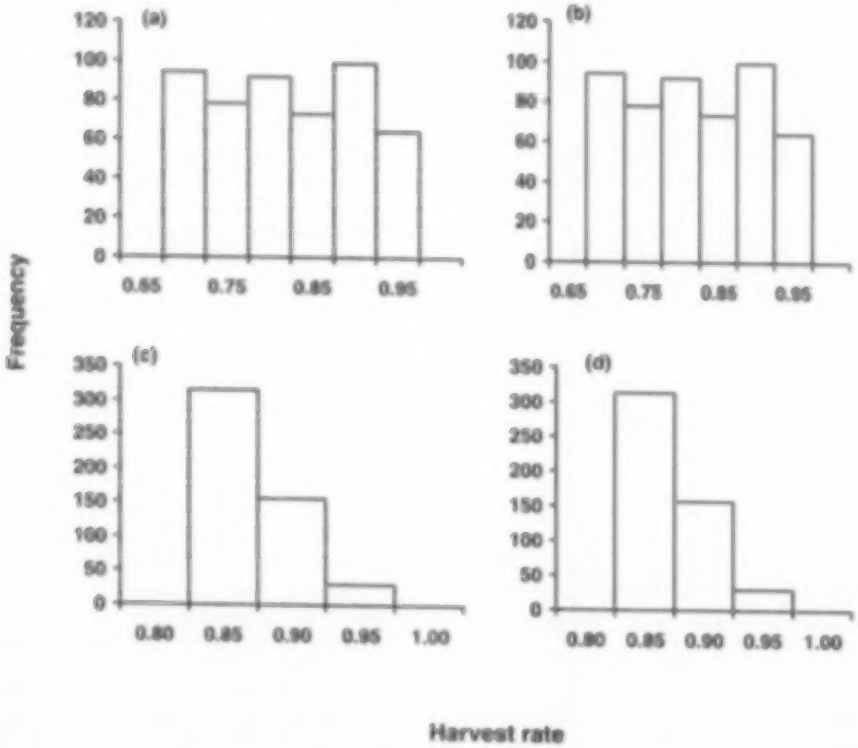
Table 8. Comparison of 2.5–97.5 percentiles, mean, median, and standard deviation of reference point estimates for Southeast Alaska and western Canada Dungeness crab for 500 randomly selected S–R shape parameter (τ) values within 0.20–0.50 and 100 perturbed recruits for 100-generation fishing at each F level.

Stock	Southeast Alaska	Southeast Alaska	Western Canada	Western Canada
L_∞ (mm CW)	165	165	155	155
T	0.4583	0.4583	0.1667	0.1667
σ_ε	0.70	0.90	0.70	0.90
M	0.47	0.47	0.91, 0.75	0.91, 0.75
$U(F_{MSY})$				
2.5%–97.5%	0.66–0.92	0.66–0.92	0.82–0.90	0.82–0.90
Mean, median	0.79, 0.79	0.79, 0.79	0.85, 0.82	0.85, 0.82
SD	0.09	0.09	0.03	0.03
$ESB(F_{MSY})/ESB(0)$				
2.5%–97.5%	0.75–0.83	0.71–0.79	0.80–0.85	0.76–0.81
Mean, median	0.79, 0.79	0.75, 0.75	0.83, 0.84	0.79, 0.79
SD	0.03	0.03	0.02	0.01
$SSB(F_{MSY})/SSB(0)$				
2.5%–97.5%	0.82–1.00	0.78–1.00	0.71–0.78	0.68–0.74
Mean, median	0.93, 0.95	0.91, 0.92	0.73, 0.72	0.70, 0.69
SD	0.06	0.08	0.02	0.02

Note: The recruits were generated from the Beverton–Holt S–R model with combined sexes as spawners and an initial male:female ratio of 1:1. The reference points were determined by maximizing the average yield at each F level and mean and median reference point values were estimated for 500 S–R curves. A BYM of 0.01 and an h of 0.15 were used. Other parameters are defined in the notation section.

Fig. 3. Distributions of harvest rate under 100-generation fishing for 500 randomly selected S–R shape parameter values under a stochastic Beverton–Holt S–R model. Histograms for (*a*) $\sigma_\varepsilon = 0.7$ and (*b*) $\sigma_\varepsilon = 0.9$ for the Southeast Alaska Dungeness crab stock; histograms for (*c*) $\sigma_\varepsilon = 0.7$ and (*d*) $\sigma_\varepsilon = 0.9$ for the western Canada Dungeness crab stock.



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Simulation results provided the following general conclusions:

First, when M was increased, $U(F_{MSY})$ increased for both species for the status quo input parameter values. For snow crab, the $U(F_{MSY})$ estimate for the eastern Canada stock was slightly higher than that for the Bering Sea stock. This was due to three reasons. (*i*) The M was lower for the Bering Sea stock than that for the eastern Canada stock. We used an M value of 0.3 for both sexes considering the longevity of snow crab (NPFMC 1999; Turnock 2003), even though Zheng (2003) estimated higher M values (0.46–0.97) for different size groups under terminal molt assumption. Zheng (2003) observed that higher M values did not improve the fit to survey abundance data over lower M values under nonterminal molt assumption. (*ii*) The handling mortality rate for the eastern Canada stock was nearly half of that for the Bering Sea stock. Our results showed that the harvest rate was inversely related to the handling mortality rate. (*iii*) The 2- to 4-year postmolt age groups were considered for yield estimation for the eastern Canada stock, whereas all groups were considered for the Bering Sea stock. When only 2- to 4-year postmolt groups were considered for the Bering Sea stock, the $U(F_{MSY})$ increased slightly.

Uncertainty in stock parameter values and a possibility of biennial spawning under certain environmental conditions dictate a precautionary approach to managing the two snow crab stocks. As a preliminary management measure, a harvest rate of 0.30 on legal males, which is closer to the 2.5 percentile values under stochastic Beverton–Holt recruitment as well as to the estimates under biennial spawning assumption, could be used as a threshold level for both stocks.

For Dungeness crab, the $U(F_{MSY})$ for the Southeast Alaska stock was lower (0.79) than that for the western Canada stock (0.85) at the current legal size exploitation because the M estimate for the Alaskan stock was lower (0.47) than that for the western Canadian stock. High M values for the western Canadian stock (0.91 and 0.75) are reasonable considering its shorter life expectancy (6 years) compared with that for the Southeast Alaska stock (10 years) and prevalence of molt-induced, short-term high mortality (Zhang et al. 2002). The comparison of modeling results for the Southeast Alaska and Fraser River Delta Dungeness crab stocks indicated that the model results were almost exclusively driven by the M and growth parameter values for the area. For example, when the model was run with a high M of 0.8 for the Southeast Alaska stock, the mean and median harvest rates reached 0.94 (±0.002). The M is known to vary considerably both temporally and spatially along the coast (Butler and Hankin 1992; Zhang et al. 2002). Therefore, using the results from this exercise for extrapolation to all the different regions of the coast should be treated with extreme caution. The mean and median harvest rates (0.85 and 0.82, respectively) from the model using Fraser River Delta information are higher than $F_{0.1}$ calculations for northern areas of British Columbia, which indicated harvest rates of 0.65–0.75 (Zhang et al. 2002). Even with uncertainty in various input parameters to the model, the Fraser River Delta crab fisheries would presently be described as being overfished. Although no reliable estimate of harvest rate is available for Dungeness crab in Southeast Alaska, recruit composition of the stock suggests that harvest rates in some years are over 0.85, which would be overexploited, as it exceeds the threshold estimate of 0.79. Similar to snow crab harvest rate recommendations, 2.5 percentile harvest rate values under stochastic Beverton–Holt recruitment, 0.66 for the Southeast Alaska stock and 0.82 for the western Canada stock, could be used as preliminary threshold RP values.

Second, when the initial ratio of prerecruit-1 males and class-1 females was changed, the RP estimates also changed. Therefore, a plausible initial male to female ratio value is needed for reliable estimation of RPs.

Third, the mean harvest rate for female-only spawners was higher than that for the combined sexes spawners. In the absence of established S–R relationships, the results from the combined sexes S–R model offer a precautionary lower $U(F_{MSY})$.

Fourth, the mean harvest rate for the Beverton–Holt S–R relationship was lower than that for the Ricker S–R model. This appeared to be a model-based result and was observed for the other king and Tanner crab (*Chionoecetes bairdi*) stocks in the Bering Sea as well (Siddeek 2002).

Fifth, for the snow crab, the mean and median nominal mature biomass ratios varied within the range 43–49% and 49–51% of the virgin biomass for varying parameter values (except the unlikely event of zero handling mortality) for the deterministic Beverton–Holt S–R relationship and 53–56% and 53–56% for the stochastic Beverton–Holt S–R model for the Bering Sea and the eastern Canada stocks, respectively. When good estimates of virgin biomass and current biomass are available, this percentage can be used to estimate $SSB(F_{MSY})$, minimum stock size threshold, and total allowable catch (Siddeek 2002). On the other hand, the stochastic S–R modeling suggested that in the absence of an F_{MSY} estimate, mainly because of lack of an S–R relationship and unavailability of biomass estimates, a suitable $F_{\%SSB(0)}$ value within the range of 53–56% could be used as a threshold level for management. For a start, a threshold fishing mortality equivalent to $F_{55\%SSB(0)}$ may be considered as a benchmark for management of less investigated snow crab stocks. A similar approach can be followed for the Dungeness crab stocks and the results suggest a threshold fishing mortality equivalent to $F_{70\%SSB(0)}$ for the western Canada stock and $F_{92\%SSB(0)}$ for the Southeast Alaska stock. However, one should be cautious when using $F_{\%SSB(0)}$ alone as a management tool because a poor estimate of M could influence its outcome (Clark 2002).

Under precautionary management, the target harvest rates should be set at lower levels to provide a buffer against overshooting $U(F_{MSY})$, perhaps at 75% of the $U(F_{MSY})$ when the stocks are near or above the MSY-producing levels, and reduced further by a proportion of current stock biomass over MSY-producing stock biomass when they are below MSY-producing levels (Restrepo and Powers 1999). The Bering Sea snow crab stock has been declared overfished and this procedure was followed in the rebuilding strategy. Based on an M value of 0.3, the harvest rate on mature male abundance of the stock at the time of the survey was set at 0.225 ($= 0.75 \times 0.3$), and a stairstep function of harvest rate based on current $SSB(F)$ and $SSB(F_{MSY})$ with a 58% maximum harvest rate cap on marketable-size male abundance was prescribed to obtain the harvestable number of marketable-size crabs from mature male abundance for rebuilding this stock

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(Zheng et al. 2002). However, the harvest rates estimated in this paper are based on marketable-size crabs at the time of fishing and the estimated median value under the Beverton–Holt S–R model is 0.34. Seventy-five percent of this estimate is 0.26. If the harvest rate on mature males recommended in the rebuilding plan is followed, then the harvest rate that is effective on marketable-size males at the time of fishing, which takes place approximately 6 months after the survey, to obtain the GHL will be much higher than 0.26, which may lead to overfishing.

A 0.32 exploitation rate on legal males was set empirically for the southern Gulf of St. Lawrence snow crab stock for a few years in the past. Loch et al. (1995, p. 262) explained the genesis of this RP as being "70% of the lower confidence limit of the exploitable biomass estimate for 1990". This RP was increased to 0.38 in 1992 and then decreased, and for the 2002 fishing season, it was suddenly hiked to over 0.50 (Hébert et al. 2003), which may have led to overfishing. Indeed, the 75% level of the mean and median harvest rate (= 0.40) at the current legal size under the Beverton–Holt S–R model is 0.30, which is close to the initial empirically set value.

Long-term success of RPs will depend on whether or not fishing is a neutral force in phenotypic and genotypic selection. If there is selection against large size-at-maturity, then yield may gradually be lost and the optimal exploitation rate for the long term might be less than predicted by the model. Some evidence of long-term declining size trends in males in heavily fished populations exists for the blue crab *C. sapidus* (Abbe 2002). Environmental and ecosystem changes may also affect the threshold values but were not considered in this modeling exercise.

There are a number of criticisms for using model-based RPs as a management procedure (Hilborn 2002). Hilborn discussed the dark side of RPs stating that virgin biomasses as well as RPs were difficult to determine and advocated use of data-based management procedures (e.g., catch rate). Indeed, quota recommendations based on purely biomass-based policy will be sensitive to changes in virgin and current biomass estimates (Clark 2002). However, in this paper, we derived F_{MSY}-based mean and median harvest rates and spawning and mature biomass ratios feasible under a broad range of S–R relationships, which are independent of the actual biomass estimate but dependent on life history parameters, as possible management procedures, especially for data- and analysis-poor crab stocks. But precise estimates of RPs by this method depend on good estimates of natural mortality, mating ratio, specific S–R relationship, and initial sex ratio. In the application of this method to snow crab and Dungeness crab stocks, some of these parameters were borrowed from similar stocks, were simply educated guesses, or considered a range of values. Greater effort should be devoted to determine reliable estimates of these parameters. Finally, because of uncertainty in input parameters and models in any stock assessment, we recommend a combination of model- and data-based approaches to set harvest rate and allowable catch and monitor the success of management decisions on crab stocks. The data-based approach should not be restricted to catch rate alone but should also include other indices, especially those related to reproduction and strength of incoming recruitment.

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Notation used in the text, tables, and appendices

t_r	relative age at recruitment in years
λ	relative maximum age of a cohort in years
$R(F)$	total number of prerecruit-1 and class-1 progenies produced by effective spawning stock biomass corresponding to fishing mortality F, ESB(F)
R_{max}	maximum R
$(ESB/R)_F$ and $(ESB/R)_{F=0}$	effective spawning stock biomass per recruit corresponding to a fishing mortality F and $F = 0$, respectively
$(ESB/R)_{ESB=0}$	effective spawning stock biomass per recruit determined as the reciprocal of the slope at the origin of the stock–recruitment (S–R) curve
$\hat{h}$	mortality rate resulting from handling of sublegal male and all female crabs
$HM1_l$	instantaneous handling mortality of male at size l
$HM2_l$	instantaneous handling mortality of female at size l
BYM	constant annual instantaneous bycatch mortality in nondirected fisheries
s_l	fishery selectivity probability at size l
$\hat{a}$	duration of average fishing period as a fraction of a year (handling and fishing mortality occur during this time period; hence, handling mortality and annual fishing mortality values are scaled to this period)
$U(F_{MSY})$	exploitation rate corresponding to F_{MSY}, equivalent to threshold harvest rate
τ	a parameter estimated from a spawning biomass per recruit ratio that influences the steepness near the origin and overall shape of the S–R curve
$P_{l,j}$	probability of crabs in a size group l' growing into a size group l
$N(F)_{l,t}$ and $N(0)_{l,t}$	abundances in numbers in a size-class l' of a cohort of new-shell crabs corresponding to a fishing mortality F (for legal males) and $F = 0$ (for females or sublegal males), respectively, in year t
$O(F)_{l,t}$ and $O(0)_{l,t}$	abundances in numbers in a size-class l' of a cohort of old-shell crabs corresponding to a fishing mortality F (for legal males) and $F = 0$ (for females or sublegal males), respectively, in year t
$S(F)_{l,t} = N(F)_{l,t} + O(F)_{l,t}$, $\bar{N}(F)_t$, and $\bar{N}(0)_t$	average abundances in numbers in a cohort corresponding to a fishing mortality F (for legal males) and $F = 0$ (for females or sublegal males), respectively, in year t
subscripts	subscripts attached to abundance notations are as follows: ipre, immature prerecruit male; ipost, immature postrecruit male; mpre, mature prerecruit male; mpost, mature postrecruit male; ic11, immature class-1 female; ic12, immature class-2 female; mc11, mature class-1 female; mc12, mature class-2 female; p, number of prerecruit-1 size intervals; q, number of recruit and postrecruit size intervals; r, number of class-1 female size intervals; s, number of class-2 female size intervals
mm_l	mature male molting probability in a size-class l' (mf_l for females)
im_l	immature male molting probability in a size-class l' (if_l for females)
a_l	immature male (or female) maturity probability in a size-class l'
MSSN(F)	sum of average mature legal and sublegal male crab abundances in number over an average fishable life span (i.e., mature male stock abundance) corresponding to a fishing mortality F on legal males
FSSN(0)	sum of average mature female crab abundances in number over an average fishable life span (i.e., mature female stock abundance) corresponding to a zero fishing mortality
CW	carapace width
L_c	minimum capture size
$\bar{B}(F)_t$ and $\bar{B}(0)_t$	average effective spawning biomasses (adjusted for male to female mating ratio) in a cohort corresponding to a fishing mortality F (for legal males) and $F = 0$ (for females or sublegal males), respectively, in year t
MSSB(F)	sum of average effective spawning biomass of mature legal and sublegal male crabs over an average fishable life span (i.e., effective spawning stock biomass of males) corresponding to a fishing mortality F on legal males
FSSB(0)	sum of average effective spawning biomass of mature female crabs over an average fishable life span (i.e., effective spawning stock biomass of females) corresponding to a zero (direct) fishing mortality on females
ESB(F), ESB(F_{MSY}), and ESB(0)	effective spawning stock biomass corresponding to a fishing mortality F, F_{MSY}, and $F = 0$, respectively, on legal males
SSB(F), SSB(F_{MSY}), and SSB(0)	nominal (unadjusted for male to female mating ratio) total mature stock biomass corresponding to a fishing mortality F, F_{MSY}, and $F = 0$, respectively, on legal males
T	time elapsed between the midmolting period (i.e., start of a biological year) and start date of a fishing period as a fraction of a year
$c(F)_t$	sum of catches in all size groups of legal males in a cohort in number corresponding to a fishing mortality F in year t
$y(F)_t$	sum of catches in all size groups of legal males in a cohort in weight corresponding to a fishing mortality F in year t

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$C(F)$	sum of $c(F)_l$ through the fishable life span (i.e., stock catch in number) from t_τ to λ.
$Y(F)$	sum of $y(F)_l$ through the fishable life span (i.e., stock catch in weight) from t_τ to λ.
α, β, γ, and θ	parameters in the S–R models
ρ	recruitment autocorrelation parameter
σ_ε	standard deviation of recruitment noise in the S–R models
j, l', and t	summation indices
e	base of natural logarithms

Appendix A. Calculation steps to determine effective spawning stock biomass per recruit of female $(ESB_{female}/R)_F$ and combined sexes $(ESB_{combined\ sexes}/R)_F$.

The following assumptions were made to simplify the derivation: (*i*) growth is constant for each time step; (*ii*) mortality takes place immediately after growth; (*iii*) maturity probability is constant for each time step; (*iv*) instantaneous bycatch mortality, BYM, is constant and independent of size, sex, and shell condition; (*v*) instantaneous natural mortality, M, is independent of shell condition; (*vi*) instantaneous fishing mortality, F, and handling mortality, HM, are size dependent; (*vii*) Recruits generated from S–R models have a constant sex ratio.

Male cohort dynamics

Male prerecruit-1 group consists of p size classes and recruits and postrecruits consist of q size classes. The following models are applicable to the size intervals.

Prerecruit-1 ($l = 1$ to p)

When $t + 1 = 0$,

(A1) $\text{Prerecruit} - 1 = S_{\text{mpre}}(0)_l + S_{\text{fmpre}}(0)_l$

where S is the sum of new- and old-shell crab abundances. When $t + 1 \geq 1$,

(A2) $$N_{\text{mpre}}(0)_{l,t+1} = \sum_{l'=1}^{l} [S_{\text{mpre}}(0)_{l',t}\text{mm}_{l'}P_{l',l} + S_{\text{fpre}}(0)_{l',t}\text{im}_{l'}a_{l'}P_{l',l}]e^{-(M+\text{HM1}_{l'}\delta+\text{BYM})}$$

(A3) $$O_{\text{mpre}}(0)_{l,t+1} = [S_{\text{mpre}}(0)_{l,t}(1-\text{mm}_l)]e^{-(M+\text{HM1}_l\delta+\text{BYM})}$$

(A4) $$N_{\text{fpre}}(0)_{l,t+1} = \sum_{l'=1}^{l} [S_{\text{fpre}}(0)_{l',t}\text{im}_{l'}(1-a_{l'})P_{l',l}]e^{-(M+\text{HM1}_{l'}\delta+\text{BYM})}$$

(A5) $$O_{\text{fpre}}(0)_{l,t+1} = [S_{\text{fpre}}(0)_{l,t}(1-\text{im}_l)]e^{-(M+\text{HM1}_l\delta+\text{BYM})}$$

Recruits and postrecruits ($l = p + 1$ to $p + q$)

When $t + 1 = 0$,

(A6) $N_{\text{mpost}}(0)_l = N_{\text{fmpost}}(0)_l = 0$

When $t + 1 = 1$,

(A7) $$N_{\text{mpost}}(0)_{l,t+1} = \sum_{l'=1}^{p} [N_{\text{mpre}}(0)_{l',t}\text{mm}_{l'}P_{l',l} + N_{\text{fpre}}(0)_{l',t}\text{im}_{l'}a_{l'}P_{l',l}]e^{-(M+\text{HM1}_{l'}\delta+\text{BYM})}$$

(A8) $$N_{\text{fpost}}(0)_{l,t+1} = \sum_{l'=1}^{p} [N_{\text{fpre}}(0)_{l',t}\text{im}_{l'}(1-a_{l'})P_{l',l}]e^{-(M+\text{HM1}_{l'}\delta+\text{BYM})}$$

When $t + 1 \geq 2$,

(A9) $$N_{\text{mpost}}(F)_{l,t+1} = \sum_{l'=1}^{p} [S_{\text{mpre}}(0)_{l',t}\text{mm}_{l'}P_{l',l} + S_{\text{fpre}}(0)_{l',t}\text{im}_{l'}a_{l'}P_{l',l}]e^{-(M+\text{HM1}_{l'}\delta+\text{BYM})} + \sum_{l'=p+1}^{l} [S_{\text{mpost}}(F)_{l',t}\text{mm}_{l'}P_{l',l} + S_{\text{fpost}}(F)_{l',t}\text{im}_{l'}a_{l'}P_{l',l}]e^{-(Fx_{l'}\delta+M+\text{BYM})}$$

(A10) $$O_{\text{mpost}}(F)_{l,t+1} = [S_{\text{mpost}}(F)_{l,t}(1-\text{mm}_l)]e^{-(Fx_l\delta+M+\text{BYM})}$$

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$$(A11)\quad N_{\text{spost}}(F)_{t,z+1} = \sum_{l=1}^{p}[S_{\text{spst}}(0)_{l,z}\text{im}_l(1-a_l)P_{l,z}]e^{-(M+\text{HM}1_l\delta+\text{BYM})} + \sum_{l=p+1}^{L}[S_{\text{spost}}(F)_{l,z}\text{im}_l(1-a_l)P_{l,z}]e^{-(Fs_l\delta+M+\text{BYM})}$$

$$(A12)\quad O_{\text{spost}}(F)_{l,z+1} = [S_{\text{spost}}(F)_{l,z}(1-\text{im}_l)]e^{-(Fs_l\delta+M+\text{BYM})}$$

Female cohort dynamics

The same set of formulas is used for female cohort abundance estimation by setting F to 0 and using female molt probability, growth increment, and maturity probability models and female instantaneous handling mortality. Note: terminal molt at maturity on male and female snow crabs can be evoked by setting the molt probability (male molt probability mm_l or female molt probability mf_j) to 0.

Legal male harvest

When $t + 1 = 0$, catch = 0. When $t + 1 \geq 1$, mature crab catch in number of crabs is

$$(A13)\quad c_{\text{mpost}}(F)_t = \sum_{j=p+1}^{p+q}\frac{Fs_j}{(Fs_j+M+\text{BYM})}N_{\text{mpost}}(F)_{j,z}e^{-MT}(1-e^{-(Fs_j+M+\text{BYM})\delta}) + \sum_{j=p+1}^{p+q}\frac{Fs_j}{(Fs_j+M+\text{BYM})}O_{\text{mpost}}(F)_{j,z}e^{-MT}(1-e^{-(Fs_j+M+\text{BYM})\delta})$$

and the corresponding catch in weight is

$$y_{\text{mpost}}(F)_t = \sum_{j=p+1}^{p+q}\frac{Fs_j}{(Fs_j+M+\text{BYM})}N_{\text{mpost}}(F)_{j,z}W_j e^{-MT}(1-e^{-(Fs_j+M+\text{BYM})\delta}) + \sum_{j=p+1}^{p+q}\frac{Fs_j}{(Fs_j+M+\text{BYM})}O_{\text{mpost}}(F)_{j,z}W_j e^{-MT}(1-e^{-(Fs_j+M+\text{BYM})\delta})$$

Immature crab catch in number of crabs is

$$(A14)\quad c_{\text{ipost}}(F)_t = \sum_{j=p+1}^{p+q}\frac{Fs_j}{(Fs_j+M+\text{BYM})}N_{\text{ipost}}(F)_{j,z}e^{-MT}(1-e^{-(Fs_j+M+\text{BYM})\delta}) + \sum_{j=p+1}^{p+q}\frac{Fs_j}{(Fs_j+M+\text{BYM})}O_{\text{ipost}}(F)_{j,z}e^{-MT}(1-e^{-(Fs_j+M+\text{BYM})\delta})$$

and the corresponding catch in weight is

$$y_{\text{ipost}}(F)_t = \sum_{j=p+1}^{p+q}\frac{Fs_j}{(Fs_j+M+\text{BYM})}N_{\text{ipost}}(F)_{j,z}W_j e^{-MT}(1-e^{-(Fs_j+M+\text{BYM})\delta}) + \sum_{j=p+1}^{p+q}\frac{Fs_j}{(Fs_j+M+\text{BYM})}O_{\text{ipost}}(F)_{j,z}W_j e^{-MT}(1-e^{-(Fs_j+M+\text{BYM})\delta})$$

Then, the total legal male catch ($C(F)$ in number and $Y(F)$ in weight) for an average fishery life span (λ) of the cohort (i.e., the stock catch) is

$$(A15)\quad C(F) = \sum_{t=t_c}^{\lambda}(c_{\text{mpost}}(F)_t + c_{\text{ipost}}(F)_t)$$

$$(A16)\quad Y(F) = \sum_{t=t_c}^{\lambda}(y_{\text{mpost}}(F)_t + y_{\text{ipost}}(F)_t)$$

MSY-level fishing mortality and harvest rate of legal males

$Y(F)$ is maximized to obtain F_{MSY} by systematically varying the F value from 0 to 5 by a step of 0.1 for a given set of fixed M (universal constant or constant specific for sex, stage, or postmolt age), h, BYM, T, and δ values. The corresponding reference point harvest rate is estimated as follows:

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$$(A17)\quad U(F_{MSY}) = \frac{C(F_{MSY})}{\sum_{t=t_1}^{\lambda}\sum_{j=p+1}^{p+q}[(N_{mpost}(F)_{j,t} + N_{lpost}(F)_{j,t})e^{-MT} + (O_{mpost}(F)_{j,t} + O_{lpost}(F)_{j,t})e^{-MT}]}$$

Average male spawner numbers

When $t + 1 \geq 0$,

$$(A18)\quad \overline{N}_{mpre}(0)_{t+1} = \sum_{f=1}^{p} N_{mpre}(0)_{f,t+1}(1 - e^{-(M+HM1_f\delta+BYM)})/(M + HM1_f\delta + BYM)$$

$$(A19)\quad \overline{O}_{mpre}(0)_{t+1} = \sum_{f=1}^{p} O_{mpre}(0)_{f,t+1}(1 - e^{-(M+HM1_f\delta+BYM)})/(M + HM1_f\delta + BYM)$$

When $t + 1 \geq 1$,

$$(A20)\quad \overline{N}_{mpost}(F)_{t+1} = \sum_{f=1}^{p} N_{mpre}(0)_{f,t+1}(1 - e^{-(M+HM1_f\delta+BYM)})/(M + HM1_f\delta + BYM) + \sum_{f=p+1}^{p+q} N_{mpost}(F)_{f,t+1}(1 - e^{-(M+Fs_f\delta+BYM)})/(M + Fs_f\delta + BYM)$$

$$(A21)\quad \overline{O}_{mpost}(F)_{t+1} = \sum_{f=1}^{p} O_{mpre}(0)_{f,t+1}(1 - e^{-(M+HM1_f\delta+BYM)})/(M + HM1_f\delta + BYM) + \sum_{f=p+1}^{p+q} O_{mpost}(F)_{f,t+1}(1 - e^{-(M+Fs_f\delta+BYM)})/(M + Fs_f\delta + BYM)$$

The sum of average mature abundances in number over the reproductive ages of male is estimated by

$$(A22)\quad MSSN(F) = \sum_{t=t_1-1}^{\lambda}(\overline{N}_{mpre}(0)_t + \overline{O}_{mpre}(0)_t) + \sum_{t=t_1}^{\lambda}(\overline{N}_{mpost}(F)_t + \overline{O}_{mpost}(F)_t)$$

No F occurs in the female average mature abundance equations; instead, $HM2_f$ occurs. The relevant equations are as follows. When $t + 1 \geq 0$,

$$(A23)\quad \overline{N}_{mc11}(0)_{t+1} = \sum_{f=1}^{r} N_{mc11}(0)_{f,t+1}(1 - e^{-(M+HM2_f\delta+BYM)})/(M + HM2_f\delta + BYM)$$

$$(A24)\quad \overline{O}_{mc11}(0)_{t+1} = \sum_{f=1}^{r} O_{mc11}(0)_{f,t+1}(1 - e^{-(M+HM2_f\delta+BYM)})/(M + HM2_f\delta + BYM)$$

When $t + 1 \geq 1$,

$$(A25)\quad \overline{N}_{mc12}(0)_{t+1} = \sum_{f=1}^{r} N_{mc11}(0)_{f,t+1}(1 - e^{-(M+HM2_f\delta+BYM)})/(M + HM2_f\delta + BYM) + \sum_{f=r+1}^{r+s} N_{mc12}(0)_{f,t+1}(1 - e^{-(M+HM2_f\delta+BYM)})/(M + HM2_f\delta + BYM)$$

$$(A26)\quad \overline{O}_{mc12}(0)_{t+1} = \sum_{f=1}^{r} O_{mc11}(0)_{f,t+1}(1 - e^{-(M+HM2_f\delta+BYM)})/(M + HM2_f\delta + BYM) + \sum_{f=r+1}^{r+s} O_{mc12}(0)_{f,t+1}(1 - e^{-(M+HM2_f\delta+BYM)})/(M + HM2_f\delta + BYM)$$

The sum of average mature abundances in number over the reproductive ages of female is estimated by

$$(A27)\quad FSSN(0) = \sum_{t=t_1-1}^{\lambda}(\overline{N}_{mc11}(0)_t + \overline{O}_{mc11}(0)_t) + \sum_{t=t_1}^{\lambda}(\overline{N}_{mc12}(0)_t + \overline{O}_{mc12}(0)_t)$$

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Effective spawning biomass

The mating ratio (the number of females that a male can mate during a spawning period) is applied to adjust the average spawning stock abundances to determine effective female (FSSB(F)), male (MSSB(F)), and total (ESB(F)) spawning stock biomass corresponding to a fishing mortality F. For example, if one male mates with three females during the breeding period, the effective spawning abundance for each sex is estimated as follows: (*i*) if FSSN(0) ≤ MSSN(F), then male effective spawning abundance is set at FSSN(0)/3 and the corresponding female value is set at FSSN(0), (*ii*) if FSSN(0) > MSSN(F) but 3 × MSSN(F) ≥ FSSN(0), then male effective spawning abundance is set at FSSN(0)/3 and the corresponding female estimate is set at FSSN(0), and (*iii*) if FSSN(0) > MSSN(F) but 3 × MSSN(F) < FSSN(0), then male effective spawning abundance is set at MSSN(F) and the corresponding female value is set at 3 × MSSN(F).

Male effective spawning biomass

The effective spawning biomass for males, MSSB(F), is estimated by the following formulas. When $t + 1 \geq 0$,

$$\text{(A28)}\quad \overline{B}_{\text{mpre}}(0)_{t+1} = \left[\sum_{f=1}^{p} N_{\text{mpre}}(0)_{f,t+1} W_f (1 - e^{-(M + \text{HM1}_f \delta + \text{BYM})})/(M + \text{HM1}_f \delta + \text{BYM}) + \sum_{f=1}^{p} O_{\text{mpre}}(0)_{f,t+1} W_f (1 - e^{-(M + \text{HM1}_f \delta + \text{BYM})})/(M + \text{HM1}_f \delta + \text{BYM})\right] \frac{\text{effective MSSN}(F)}{\text{MSSF}(F)}$$

When $t + 1 \geq 1$,

$$\text{(A29)}\quad \overline{B}_{\text{mpost}}(F)_{t+1} = \left[\sum_{f=1}^{p} N_{\text{mpre}}(0)_{f,t+1} W_f (1 - e^{-(M + \text{HM1}_f \delta + \text{BYM})})/(M + \text{HM1}_f \delta + \text{BYM}) + \sum_{f=p+1}^{p+q} N_{\text{mpost}}(F)_{f,t+1} W_f (1 - e^{-(M + \text{Fs}_f \delta + \text{BYM})})/(M + Fs_f \delta + \text{BYM}) + \sum_{f=1}^{p} O_{\text{mpre}}(0)_{f,t+1} W_f (1 - e^{-(M + \text{HM1}_f \delta + \text{BYM})})/(M + \text{HM1}_f \delta + \text{BYM}) + \sum_{f=p+1}^{p+q} O_{\text{mpost}}(F)_{f,t+1} W_f (1 - e^{-(M + \text{Fs}_f \delta + \text{BYM})})/(M + Fs_f \delta + \text{BYM}\right] \frac{\text{effective MSSN}(F)}{\text{MSSN}(F)}$$

Therefore,

$$\text{(A30)}\quad \text{MSSB}(F) = \sum_{t=t_r-1}^{\lambda} \overline{B}_{\text{mpre}}(0)_t + \sum_{t=t_r}^{\lambda} \overline{B}_{\text{mpost}}(F)_t$$

Female effective spawning biomass

Corresponding equations for female effective spawning biomass, FSSB(0), are as follows. When $t + 1 \geq 0$,

$$\text{(A31)}\quad \overline{B}_{\text{mc11}}(0)_{t+1} = \left[\sum_{f=1}^{r} N_{\text{mc11}}(0)_{f,t+1} W_f (1 - e^{-(M + \text{HM2}_f \delta + \text{BYM})})/(M + \text{HM2}_f \delta + \text{BYM}) + \sum_{f=1}^{r} O_{\text{mc11}}(0)_{f,t+1} W_f (1 - e^{-(M + \text{HM2}_f \delta + \text{BYM})})/(M + \text{HM2}_f \delta + \text{BYM})\right] \frac{\text{effective FSSN}(0)}{\text{FSSN}(0)}$$

When $t + 1 \geq 1$,

$$\text{(A32)}\quad \overline{B}_{\text{mc12}}(0)_{t+1} = \left[\sum_{f=1}^{r} N_{\text{mc11}}(0)_{\text{mc11}f,t+1} W_f (1 - e^{-(M + \text{HM2}_f \delta + \text{BYM})})/(M + \text{HM2}_f \delta + \text{BYM}) + \sum_{f=1}^{r} O_{\text{mc11}}(0)_{f,t+1} W_f (1 - e^{-(M + \text{HM2}_f \delta + \text{BYM})})/(M + \text{HM2}_f \delta + \text{BYM})\right] \frac{\text{effective FSSN}(0)}{\text{FSSN}(0)}$$

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$$+\left[\sum_{l=r+1}^{r+s} N_{\text{mcl2}}(0)_{l,s+1} W_l (1-e^{-(M+\text{HM2}_l\delta+\text{BYM})})/(M+\text{HM2}_l\delta+\text{BYM}) \right.$$

$$\left. + \sum_{l=r+1}^{r+s} O_{\text{mcl2}}(0)_{l,s+1} W_l (1-e^{-(M+\text{HM2}_l\delta+\text{BYM})})/(M+\text{HM2}_l\delta+\text{BYM}) \right] \frac{\text{effective FSSN(0)}}{\text{FSSN(0)}}$$

Therefore,

$$\text{(A33)}\quad \text{FSSB(0)} = \sum_{l=l_r-1}^{\lambda} \overline{B}_{\text{mcl1}}(0)_l + \sum_{l=l_r}^{\lambda} \overline{B}_{\text{mcl2}}(0)_l$$

The effective spawning stock biomasses per recruit of female and combined sexes are determined by

$$\text{(A34)}\quad (\text{ESB}_{\text{female}}/R)_F = \text{FSSB(0)}/R_{\text{female}}(F)$$

$$\text{(A35)}\quad (\text{ESB}_{\text{combined sexes}}/R)_F = (\text{MSSB}(F) + \text{FSSB(0)})/R_{\text{combined sexes}}(F)$$

The effective total spawning stock biomass, ESB(F), is

$$\text{(A36)}\quad \text{ESB}(F) = \text{FSSB(0)} + \text{MSSB}(F)$$

The nominal total mature stock biomass, SSB(F), is calculated using eq. A36 ignoring mating ratio.

Auxiliary models

Weight – carapace width (CW) relationship

For estimating a mean weight W_l of a CW interval l (Beyer 1987),

$$\text{(A37)}\quad W_l = \left(\frac{1}{\text{CW}_{\text{up}} - \text{CW}_{\text{low}}}\right)\left(\frac{a}{b+1}\right)\left(\text{CW}_{\text{up}}^{b+1} - \text{CW}_{\text{low}}^{b+1}\right)$$

where

$$\text{(A38)}\quad W = a\text{CW}^b$$

and CW_{up} and CW_{low} are the upper and lower size limits, respectively, of a CW interval, and a and b are model parameters.

Handling mortality on sublegals

The $\text{HM}i_l$ (i = 1 for males and i = 2 for females) at CW interval l is defined as a function of Fs_l, h, and δ, ignoring M and BYM as follows:

$$1 - e^{-\text{HM}i_l \cdot \delta} = h(1 - e^{-Fs_l \cdot \delta})$$

Therefore,

$$\text{(A39)}\quad \text{HM}i_l = -\frac{1}{\delta}\ln[1 - h(1 - e^{-Fs_l \cdot \delta})]$$

Note that F accounts for legal and sublegal catches, but only an h proportion of sublegal male and female eventually dies as a result of handling and throwing them back to sea. The selectivity s_l applies to a range of sizes covering legal and sublegal crabs.

$\mathbf{P}_{l,k}$ *determination*

Annual growth increment (x) of crabs is assumed to have a normal distribution with a mean growth increment G_l and a standard deviation σ_l. Then:

$$\text{(A40)}\quad P_{l,k} = \frac{\int_{l_k - \tau_l}^{l_{k+1} - \tau_l} e^{\frac{-(x - G_l)^2}{2\sigma_l^2}} dx}{\sum_{k=1}^{n} \int_{l_k - \tau_l}^{l_{k+1} - \tau_l} e^{\frac{-(x - G_l)^2}{\sigma_l^2}} dx}$$

where

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(A41) $G_l = a1 + b1\bar{l}$

and n is the total number of CW intervals available in a cohort for P_{fj} estimation, σ_l is estimated from G_l assuming a 10% coefficient of variation, l_2 and l_1 are the lower and upper limits, respectively, of a receiving CW interval l for P_{fj} estimation, $\tau_{\bar{l}}$ is the midwidth of a providing CW interval $\bar{l}$ for P_{fj} estimation, $\bar{l}$ is the midwidth of a width interval l, and $a1$ and $b1$ are linear model parameters.

Pot selectivity

A double logistic function is used to get a dome-shaped pot selectivity (s_l) curve for snow crab:

(A42) $$s_l = \left(\frac{1}{1 + e^{-a5(l-b5)}}\right)\left(\frac{1}{1 + e^{c(l-d)}}\right)$$

where $a5$, $b5$, c, and d are model parameters and l is the size. A linear function is used for pot selectivity of Dungeness crab:

(A43) $s_l = a4 - b4\,(157.5 - l)$

where $a4$ and $b4$ are linear model parameters and l is the size.

Molt probability

Molt probability is given by

(A44) $$f(l) = 1 - \frac{1}{1 + e^{-a3(l-b3)}}$$

where $f(l)$ can be mm_l, im_l, mf_l, or if_l; $a3$ and $b3$ are model parameters; and l is the size.

Maturity probability

Maturity probability (a_l) for snow crab males or females is

(A45) $$a_l = \frac{1}{1 + e^{-a2(l-b2)}}$$

where $a2$ and $b2$ are model parameters and l is the size.

References

Beyer, J.E. 1987. On length–weight relationships: Part 1: computing the mean weight of the fish in a given length class. ICLARM Fishbyte, **5**: 11–13.

Appendix B

Appendix appears on the following page.

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Table B1. Input parameters of Bering Sea snow crab for reference point estimation.

	Male		Female		
Parameter	Prerecruit-1	Recruit and postrecruit	Class-1	Class-2	Remarks
Size range (mm CW)	82–101	102–131	50–59	60–69	
Natural mortality rate (M)	0.30	0.30	0.30	0.30	NPFMC 1999
Handling mortality rate (h)	0.25	0.25	0.25	0.25	Zheng et al. 2002
Bycatch mortality (BYM)	0.01	0.01	0.01	0.01	Siddeek 2002
Growth increment model: $a1$, $b1$	8.8706, 0.1742	8.8706, 0.1742	11.68, 0.0	11.68, 0.0	Turnock 2003
Maturity probability: $a2$, $b2$	0.12, 88.00	0.12, 88.00	0.1628, 48.7665	0.1628, 48.7665	Siddeek 2003*b*
Molt probability: $a3$, $b3$					
Immature	0.0498,140.2407	0.0498,140.2407	100% molt	100% molt	Turnock 2003
Mature	0% molt	0% molt	0% molt	0% molt	Turnock 2003
Weight–length model: a, b	0.00023, 3.12948	0.00023, 3.12948	0.00253, 2.56427	0.00253, 2.56427	Somerton 1981
Pot selectivity probability: $a5$, $b5$, c, d					
Mature new shell	0.2379, 102.2655, 0.3458, 129.23	0.2379, 102.2655, 0.3458, 129.23			B.J. Turnock (National Marine Fisheries Service, 7600 Sand Point Way NE, Seattle, WA 98115, USA, unpublished data)
Mature old shell	0.189, 104.2308, 0.1498, 109.578	0.189, 104.2308, 0.1498, 109.578	0.2573, 67.282, −1.0, 0.0	0.2573, 67.282, −1.0, 0.0	B.J. Turnock (unpublished data)
Immature new/old shell	0.1 × mature selectivity	0.1 × mature selectivity	0.1 × mature selectivity	0.1 × mature selectivity	Appendix B (Table B2)
Male:female mating ratio					
Primiparous	1:4	1:9			Appendix B (Table B2)
Multiparous	1:3	1:6			

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Table B2. Input parameters of eastern Canada snow crab for reference point estimation.

	Male		Female		
Parameter	Prerecruit-1	Recruit and postrecruit	Class-1	Class-2	Remarks
Size range (mm CW)	75–94	95–134	45–54	55–69	
Natural mortality rate (M)	0.2 (postmolt 1–3 years) 0.5 (postmolt 4 years) 3.0 (postmolt 5 years)	0.1 (postmolt 1–3 years) 0.2 (postmolt 4 years) 0.5 (postmolt 5–6 years) 3.0 (postmolt 7–9 years)	0.15 (postmolt 1–3 years) 0.35 (postmolt 4 years) 0.7 (postmolt 5–6 years) 3.0 (postmolt 7 years)	0.15 (postmolt 1–3 years) 0.35 (postmolt 4 years) 0.7 (postmolt 5–6 years) 3.0 (postmolt 7 years)	B. Sainte-Marie (preliminary estimates from unpublished tag–recapture data)
Handling mortality rate (h)	0.12	0.12	0.12	0.12	Dufour et al. 1997
Bycatch mortality (BYM)	0.01	0.01	0.01	0.01	Appendix B (Table B1)
Growth increment model: $a1$, $b1$	8.573, 0.11	8.573, 0.11	3.503, 0.104	3.503, 0.104	Sainte-Marie et al. 1995; Alunno-Bruscia and Sainte-Marie 1998
Maturity probability: $a2$, $b2$	0.25, 75.00	0.25, 75.00	0.45, 48.00	0.45, 48.00	B. Sainte-Marie (unpublished data)
Weight–length model: a, b	0.000313, 3.062	0.000313, 3.062	0.00097, 2.745	0.00097, 2.745	B. Sainte-Marie (unpublished data for intact mature males and females of shell condition 2)
Pot selectivity probability: $a5$, $b5$, c, d					
Mature new shell	0.2039, 78.8002, 0.1064, 31.5604	0.2039, 78.8002, 0.1064, 31.5604	Zero selectivity	Zero selectivity	Estimates for males from data in Hoenig and Dawe (1991) and B. Sainte-Marie (unpublished data)
Mature old shell	0.2039, 78.8002, 0.1064, 31.5604	0.2039, 78.8002, 0.1064, 31.5604	Zero selectivity	Zero selectivity	
Immature new/old shell	0.1 × mature selectivity	0.1 × mature selectivity	0.1 × mature selectivity	0.1 × mature selectivity	
Molt probability					Terminal molt: Conan and Comeau 1986; Sainte-Marie et al. 1995. Mean incidence of skip-molting from Comeau et al. (1998)
Immature	70% molt	70% molt	70% molt	70% molt	
Mature	0% molt	0% molt	0% molt	0% molt	
Male:female mating ratio					Rondeau and Sainte-Marie 2001; B. Sainte-Marie (unpublished data)
Primiparous	1:4	1:9			
Multiparous	1:3	1:6			

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Table B3. Input parameters of Southeast Alaska Dungeness crab for reference point estimation.

Parameter	Male		Female		Remarks
	Prerecruit-1	Recruit and postrecruit	Class-1	Class-2	
Size range (mm CW)	135–164	165–224	70–84	85–169	
Natural mortality rate (M)	0.47	0.47	0.47	0.47	Preliminary estimate from tag–recapture data (G. Bishop, unpublished data)
Handling mortality rate (h)	0.15	0.15	0.15	0.15	Appendix B (Table B4)
Bycatch mortality (BYM)	0.01	0.01	0.01	0.01	Appendix B (Table B1)
Growth increment model: $a1$, $b1$	29.91, 0.0	29.91, 0.0	28.5364, –0.1027	28.5364, –0.1027	Tag–recapture data (G. Bishop, unpublished data); Koeneman 1985
Maturity probability	100% mature	100% mature	100% mature	100% mature	Appendix B (Table B4)
Molt probability: $a3$, $b3$					
Immature	100% molt	100% molt	100% molt	100% molt	Appendix B (Table B4)
Mature	1.974, 164.6285	1.974, 164.6285	100% molt	100% molt	Tag–recapture data (G. Bishop, unpublished data)
Weight–length model: a, b	0.0002, 2.9348	0.0002, 2.9348	0.00037, 2.8339	0.00037, 2.8339	Appendix B (Table B4)
Pot selectivity probability: $a4$, $b4$					
Mature new/old shell	$a4$ = 1.0, $b4$ = 0.037 when 130 ≤ CW < 155; $b4$ = 0.0 when CW > 155	$a4$ = 1.0, $b4$ = 0.037 when 30 ≤ CW < 155; $b4$ = 0.0 when CW > 155	$a4$ = 1.0, $b4$ = 0.037 when 130 ≤ CW < 155; $b4$ = 0.0 when CW > 155	$a4$ = 1.0, $b4$ = 0.037 when 130 ≤ CW < 155; $b4$ = 0.0 when CW > 155	Appendix B (Table B4)
Immature new/old shell	0.1 × mature selectivity	0.1 × mature selectivity	0.1 × mature selectivity	0.1 × mature selectivity	Appendix B (Table B2)
Male:female mating ratio					
Primiparous and multiparous	1:3	1:3			Preliminary value

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Table B4. Input parameters of western Canada Dungeness crab for reference point estimation.

	Male		Female		
Parameter	Prerecruit-1	Recruit and postrecruit	Class-1	Class-2	Remarks
Size range (mm CW)	130–154	155–194	105–119	120–149	
Natural mortality rate (M)	0.91	0.75	0.91	0.75	Z. Zhang and J. Boutillier (unpublished data)
Handling mortality rate (h)	0.15	0.15	0.15	0.15	Zhang et al. 2002
Bycatch mortality (BYM)	0.01	0.01	0.01	0.01	Appendix B (Table B1)
Growth increment model: $a1$, $b1$	18.07, 0.069	18.07, 0.069	32.35, –0.136	32.35, –0.136	Smith and Jamieson 1989
Maturity probability	100% mature	100% mature	100% mature	100% mature	Male mature >115.9 mm CW and female mature >90.8 mm CW (Butler 1961)
Molt probability: $a3$, $b3$					
Immature	100% molt	100% molt	100% molt	100% molt	Smith and Jamieson 1989; Zhang et al. 2002
Mature	0.08774, 172.4828	0.08774, 172.4828	100% molt	100% molt	
Weight–length model: a, b	0.0002, 2.9348	0.0002, 2.9348	0.00037, 2.8339	0.00037, 2.8339	Zhang et al. 2002
Pot selectivity probability: $a4$, $b4$					
Mature new/old shell	$a4$ = 1.0, $b4$ = 0.037 when 130 ≤ CW < 155; $b4$ = 0.0 when CW > 155	$a4$ = 1.0, $b4$ = 0.037 when 130 ≤ CW < 155; $b4$ = 0.0 when CW > 155	$a4$ = 1.0, $b4$ = 0.037 when 130 ≤ CW < 155; $b4$ = 0.0 when CW > 155	$a4$ = 1.0, $b4$ = 0.037 when 130 ≤ CW < 155; $b4$ = 0.0 when CW > 155	Zhang et al. 2002
Immature new/old shell	0.1 × mature selectivity	0.1 × mature selectivity	0.1 × mature selectivity	0.1 × mature selectivity	Appendix B (Table B2)
Male:female mating ratio					
Primiparous and multiparous	1:3	1:3			Preliminary value

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Regular papers

Articles ordinaires

Predicting benefits of spawning-habitat rehabilitation to salmonid (*Oncorhynchus* spp.) fry production in a regulated California river

Joseph E. Merz, Jose D. Setka, Gregory B. Pasternack, and Joseph M. Wheaton

Abstract: We tested the hypothesis that spawning-bed enhancement increases survival and growth of chinook salmon (*Oncorhynchus tshawytscha*) embryos in a regulated California stream with a gravel deficit. We also examined how 12 physical parameters correlated within spawning sites and how well they predicted survival and growth of chinook salmon and steelhead (*Oncorhynchus mykiss*) embryos. Salmon embryos planted in enhanced gravels had higher rates of survival to the swim-up stage than embryos planted in unenhanced spawning gravels. No significant increase in growth was observed. Intergravel temperature and substrate size were strongly correlated with distance downstream from the lowest nonpassable dam. Intergravel turbidity and total suspended and volatile solids were also strongly correlated. Multiple-regression models were built with a combination of physical measurements to predict survival and length of salmon and steelhead embryos. Survival models accounted for 87% of the variation around the mean for salmon and 82% for steelhead. Growth models accounted for 95% of the variation around the mean for salmon and 89% for steelhead. These findings suggest that spawning-bed enhancement can improve embryo survival in degraded habitat. Additionally, measurements of a suite of physical parameters before and after spawning-bed manipulation can accurately predict benefits to target species.

Résumé : Nous avons éprouvé l'hypothèse selon laquelle l'aménagement des sites de reproduction augmente la survie et la croissance des embryons du saumon quinnat (*Oncorhynchus tshawytscha*) dans un cours d'eau de Californie soumis à la régulation et ayant une pénurie de gravières. Nous avons aussi déterminé la corrélation entre 12 variables physiques dans les sites de fraye et examiné comment elles peuvent prédire la survie et la croissance des embryons de saumons quinnat et de truites arc-en-ciel anadromes (*Oncorhynchus mykiss*). Les oeufs de saumons insérés dans des gravières améliorées ont une meilleure survie jusqu'au stade du début de la nage que ceux qui sont mis dans des gravières de fraye non améliorées. Il n'y a pas d'accélération significative de la croissance. La température dans le gravier et la taille du substrat sont en forte corrélation avec la distance en aval du barrage infranchissable le plus en aval. La turbidité dans le gravier, les solides totaux en suspension et les solides volatils affichent aussi la même forte corrélation. L'élaboration de modèles de régression multiple basés sur une combinaison de mesures physiques permettent de prédire la survie et la longueur des embryons de saumons quinnat et de truites arc-en-ciel anadromes. Les modèles de survie expliquent 87 % de la variation autour de la moyenne chez le saumon et 82 % chez la truite. Les modèles de croissance expliquent 95 % de la variation autour de la moyenne chez le saumon et 89 % chez la truite. Ces résultats montrent que l'amélioration des sites de fraye dans les habitats dégradés peut accroître la survie des embryons. De plus, la mesure des variables physiques avant et après la manipulation des sites de fraye peut permettre de prédire les avantages escomptés pour les espèces visées par l'aménagement.

[Traduit par la Rédaction]

Introduction

Salmonids have specific substrate and water-quality requirements for successful spawning, incubation, and embryo development. Riverine salmonids typically spawn in cool, clear, well-oxygenated streams with distinct depth, current velocity, and gravel size for each species (Bjornn and Reiser 1991; Groot and Margolis 1991). Salmonid eggs and embryos remain in the gravel for a relatively long time, ranging between roughly 2 and 8 months. The length of time between egg deposition and alevin emergence depends on species, redd location, and numerous physical parameters

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(DeVries 1997). Timing of spawning, egg burial depth, and embryo development are tied to the dynamic hydrologic regime of a river, including disturbances such as streambed scour (Montgomery et al. 1999).

Interannual mobilization of channel-bed sediment provides renewal of substrate conditions, and infrequent large floods reset spatially complex channel morphology (Trush et al. 2000). Alteration of flow, sediment transport, and continuity of river systems by dams, water diversions, levees, armoured banks, and mining may have deleterious affects on these processes, impacting upon one or more salmonid life stages (Nelson et al. 1987; Heaney et al. 2001; Soulsby et al. 2001). Elimination of a natural flow and sediment transport regime causes channel stabilization and narrowing, reduced formation of point gravel bars and secondary channels, accumulation of finer sediment in gravels, and reduced water quality (Poff et al. 1997). These physical degradations contribute to decreased substrate permeability and dissolved oxygen content (DO). Impaired water quality is presumed to cause a decrease in the health and survival of developing salmonid embryos within the substrate (Olsson and Persson 1988; Reiser and White 1988; Beacham and Murray 1990).

Since the early 1970s, numerous projects have been undertaken to ameliorate anthropogenic impacts on indigenous salmonid populations (House 1996; Scruton et al. 1997). In the Central Valley of California, 73 spawning habitat rehabilitation projects on 19 different rivers were carried out between 1976 and 1999, but their success has been poorly evaluated (Kondolf et al. 1996; Wheaton 2003). Nevertheless, concerns over the fate of California Central Valley steelhead (*Oncorhynchus mykiss*) and several runs of chinook salmon (*Oncorhynchus tshawytscha*) resulted in the United States National Marine Fisheries Service (NOAA) listing these populations as threatened or endangered under the Endangered Species Act (NOAA 1994, 1998). Salmonid spawning-habitat rehabilitation within California has received increasing attention as a tool to enhance these dwindling populations (Buer et al. 1981; Kondolf and Mathews 1993; California Department of Water Resources 2002). Wheaton (2003) developed a systematic approach to designing salmon spawning habitat rehabilitation projects using spawning-bed enhancement. While gravel augmentation typically entails dumping of appropriate materials in or near the channel to allow distribution via stream flow, spawning-bed enhancement involves placement of gravel as specific bed features (typically riffles or bars), potentially providing immediate spawning habitat. Merz and Setka (2004) showed that spawning-bed enhancement not only attracted spawning salmon to previously unused areas, but improved intergravel physical parameters associated with spawning and embryo development. Spawning-bed enhancement has been shown to benefit nontarget aquatic fauna as well (Merz and Chan 2004). Yet there is much uncertainty as to how well projects mitigate degradation of spawning habitat or improve survival of developing embryos (Roni et al. 2002). Additional research is needed to evaluate how substrate and associated hyporheic environment directly influence embryo survival (Kondolf et al. 1996; Merz and Setka 2004). In this paper, results from two embryo-survival experiments are reported. In the first experiment, we test the hypothesis that spawning-bed enhancement increases survival and growth of riverine chinook salmon embryos to the swim-up stage. In the second experiment, we propose embryo survival and growth models based on measurable physical parameters. We then test the validity of four multiple-regression models to predict the benefits of spawning-habitat enhancement on developing chinook salmon and steelhead embryos in a regulated California river.

Material and methods

Study site

The Mokelumne River, California, drains approximately 1624 km^2 of the central Sierra Nevada. Sixteen major dams or diversions, including the 0.24-km^3 Pardee and the 0.51-km^3 Camanche reservoirs, have dramatically altered the flow regime of the lower Mokelumne River (LMR) (Pasternack et al. 2004). Prior to completion of the Camanche Dam in 1964, annual peaks exceeded 200 $m^3 \cdot s^{-1}$ for 21 of 57 years. Since 1964, annual peaks have never exceeded 200 $m^3 \cdot s^{-1}$, with the discharges associated with the 2-, 5-, 10-, and 100-year recurrence intervals decreased by 67%, 59%, 73%, and 75%, respectively.

The LMR is approximately 54 km of regulated river between Camanche Dam, a nonpassable barrier to anadromous fish, and its confluence with the Sacramento – San Joaquin Delta. The river between Camanche Dam and Lake Lodi (Fig. 1), is characterized by alternating bar-complex and flat-water habitats, and is above tidal influence, with a gradient of approximately 0.00017. The drainage consists of 87 km^2 of mostly agricultural and urbanized land. Several small streams and storm drains enter the lower river. At least 35 fish species occur in the LMR, including two native anadromous salmonids, fall-run chinook salmon, and winter steelhead (Merz 2001). Both populations are supplemented by Mokelumne River Fish Hatchery (MRFH) production and fish imported from the Feather River and Nimbus (American River) hatcheries. Most chinook salmon and steelhead spawning on the LMR now takes place in the 14-km reach immediately below Camanche Dam.

Compared with other major barriers on Sierra rivers, Camanche Dam is positioned in an area of relatively low elevation and relief. Accordingly, slopes throughout the current spawning reaches remain low (ranging from 0.0005 to 0.0020). Tailings from abandoned gravel-mining operations are frequent along the upper 11 km of the LMR. While many of the tailings are isolated from the river by berms and levees, several large pits are now incorporated into the main river channel. It has been estimated that approximately 80% of historical spawning habitat is now inaccessible, owing to construction of Camanche Dam, and remaining habitat quality is a limiting factor to Mokelumne River salmonid production, second only to ocean harvest (Menchen 1961; Federal Energy Regulatory Commission 1993). East Bay Municipal Utility District, owner and operator of Camanche Dam, has placed over 11 000 m^3 of gravel at 12 spawning-bed enhancement sites along the LMR since 1991 and has a monitoring program encompassing all of these projects that will extend to at least 2009 (Pasternack et al. 2004). The projects typically consist of placing approximately 350–1200 m^3 of washed river rock in berms, staggered bar, riffle, or complex channel geometry configurations to improve

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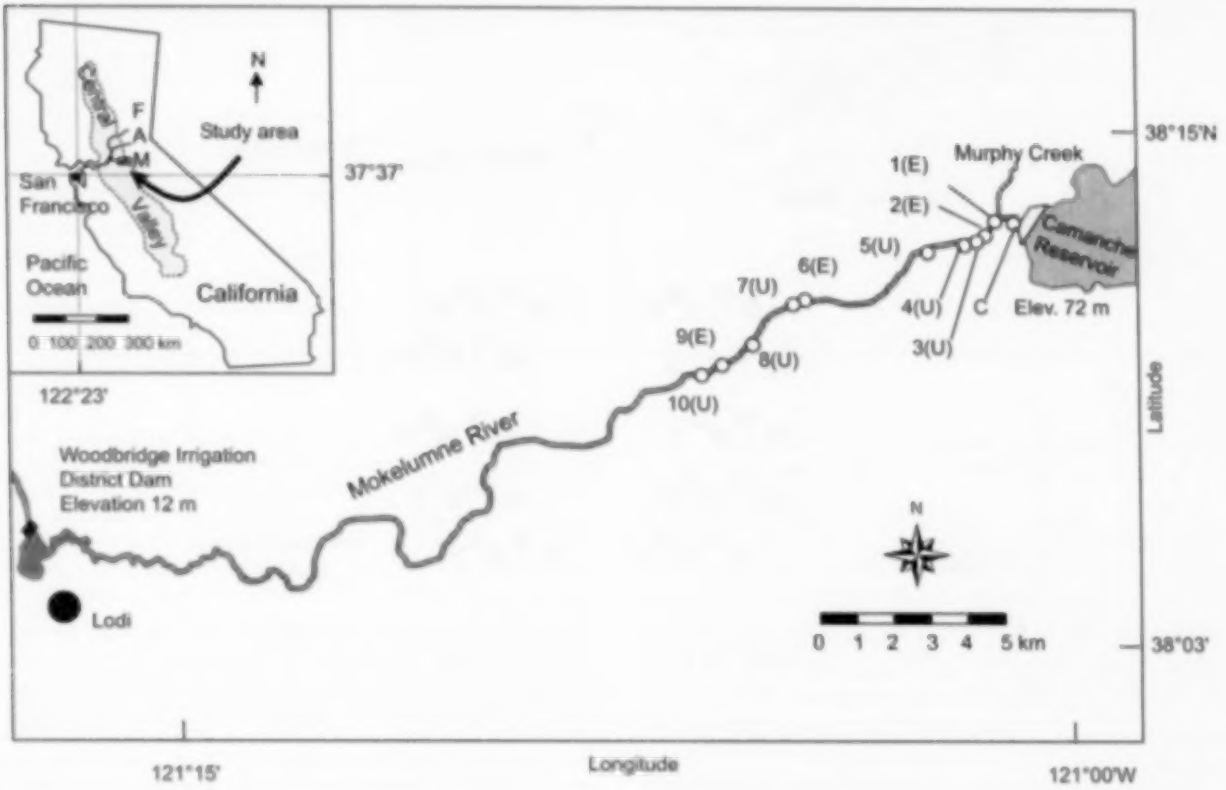
Fig. 1. Locations of 10 egg-tube study sites (○) within the lower Mokelumne River, California. C, Mokelumne River Hatchery (control); E, enhanced site; U, unenhanced site; F, Feather River; A, American River; M, Lower Mokelumne River.



spawning habitat. Chinook salmon and steelhead typically begin spawning in the new gravels within 3–24 months of gravel placement. For this study, 10 sites were evaluated based on access and how many could be assessed within a single day. The sites are spread out within the upper 11.3 km of the LMR, four of them being spawning bed enhancement sites (Fig. 1).

Egg-incubation tubes

The focus of the first experiment was to compare survival and growth (as indicated by length) of chinook salmon embryos in enhanced and unenhanced spawning gravel sites. The second experiment was conducted to develop a predictive model of chinook salmon and steelhead survival and growth using associated physical parameters within spawning beds. In both experiments, egg-incubation tubes were buried in gravels to test survival and growth of fertilized eggs and embryos.

Egg tubes were constructed of standard dimension ratio 35-polyvinyl chloride (PVC) pipe with two PVC caps to close the tube ends (Fig. 2). Eighteen, evenly spaced, 19-mm-diameter holes were drilled into each tube. The tube's inner surface was covered with 0.35 mm mesh plastic screen typically used for egg incubation in steelhead and chinook salmon hatcheries (Leitritz and Lewis 1980). An artificial "redd" was constructed at each site for egg-tube placement. A series of depressions were made by hand in the gravel streambed for each set of egg tubes (Fig. 2). Pockets were constructed in an upstream progression, following the description of DeVries (1997). At each study site, egg-incubation tubes were buried horizontally and perpendicular to stream flow at a depth of 22 cm, the approximate depth of egg pockets in chinook salmon and steelhead redds according to Healey (1991) and Montgomery et al. (1999). Bed material from subsequent pockets was used to cover each egg tube.

Experiment 1: survival and growth in enhanced versus unenhanced sites

To compare survival of chinook salmon embryos in enhanced and unenhanced gravel sites, egg tubes were buried at four enhanced-substrate locations (constructed between 1994 and 2001) and six unenhanced-substrate locations within the LMR (Fig. 1). Unenhanced sites were selected on the basis of consistent spawning use by chinook salmon and accessibility. Ten tubes with approximately 200 chinook salmon eggs each from the MRFH were buried at each site. A control group of 2000 eggs was placed in incubation tubes (200 eggs each) at the MRFH to monitor embryo development. Eggs were taken from approximately 22 female chinook salmon at the MRFH on 21 November 2001. Fertilized eggs were "eyed" and 18 days old (average hatchery water

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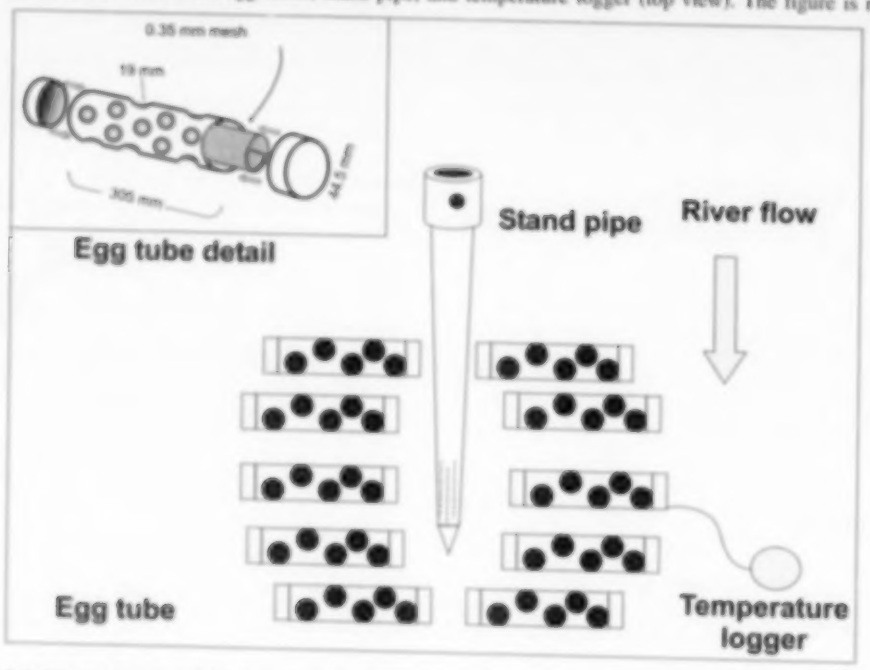
Fig. 2. Diagram of constructed "redd" with egg tubes, stand pipe, and temperature logger (top view). The figure is not drawn to scale.



temperature was 12.3 °C) when placed in the egg tubes and buried in the gravel. MRFH water is sand-filtered and piped from Camanche Reservoir.

Experiment two: predictive models of survival and growth

To test predictive models of chinook salmon and steelhead embryo survival and growth from associated physical measurements, approximately 20 000 chinook salmon and steelhead embryos were buried in egg tubes at various spawning habitats located throughout the LMR (see Habitat selection and evaluation below). Five tubes with approximately 200 eyed chinook salmon embryos and five tubes with approximately 200 eyed steelhead embryos were buried at each site. A control group of five chinook salmon egg tubes and five steelhead egg tubes (200 embryos each) were placed in rearing troughs at the MRFH to monitor embryo development and survival. Chinook salmon eggs were taken from 15 female salmon spawned on 23 December 2001 at the MRFH. Fertilized eggs were eyed and 18 days old (average hatchery water temperature was 10.12 °C) when placed in egg tubes and buried in the gravel on 9 January 2002. An insufficient number of steelhead spawned at the MRFH to provide embryos for this study, therefore eggs were taken from 12 female steelhead spawned on 18 December 2001 at the Feather River Hatchery, California. Fertilized steelhead eggs were approximately 22 days old when placed in the egg tubes and buried in the gravel on 9 January 2002 (average hatchery water temperature was 10.3 °C).

Habitat selection and evaluation

For experiment 2, 10 sites were selected within the upper 11.3 km of the LMR, based on historical spawning use and enhancement activities (Fig. 1). Although, the sites were located in the vicinity of experiment 1 sites, the sites did not overlap and were not selected on the basis of enhanced versus unenhanced gravels. The 10 sites each consisted of similar riffle morphologies with comparable substrate compositions (D_{50} = 150–450 mm gravels), channel slopes (0.002–0.006) and hydraulic conditions (shallow (<0.36 m), and swift current (>0.6 m·s^{-1}). Hydraulics at each site were crudely characterized from one point measurement of depth and velocity positioned between the egg tube placement locations (at the standpipe location; Fig. 2). This measurement was performed on 9 December 2001 during a discharge of 6.5 m^3·s^{-1}, which was representative of hydraulics experienced throughout the incubation period. Depth was recorded from a top-setting velocity rod and depth-averaged velocity was approximated by assuming a logarithmic velocity profile and taking a measurement at 60% of the depth with an electromagnetic Marsh McBirney Flo-Mate velocimeter.

Substrate evaluation

Both surface and subsurface grain-size distributions were used to characterize the substrate during the post-study period (after egg-tube removal) at each site. Grain-size distributions were assumed not to have changed from pre- to post-analysis based on previous studies (Merz and Setka 2004). Subsurface samples were collected at the location of the standpipe at each site using a McNiel core sampler (St-Hilaire et al. 1997). Samples were placed in sealed containers and transported to the laboratory for analysis. Substrate was sieved through screens of the following sizes: 0.5, 1.0, 2.4, 4.7, 9.5, 12.7, 15.9, 22.2, 31.8, 44.5, 63.5, 88.9, 127.0, 177.8, and 254.0 mm. Each size class was weighed and recorded. Residual water and associated suspended sediment was poured through 15-cm No. 595 filter paper. The paper and sediment residual was dried at 70 °C for 24 h, weighed,

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Table 1. Observed survival rates and total lengths (TL) of chinook salmon embryos incubated in egg tubes from 12 December 2001 through 7 January 2002 and from 9 January through 31 January 2002 at the Mokelumne River Fish Hatchery and at four enhanced and five unenhanced spawning sites.

Experiment/group	Species	Mean survival rate (%)	SE*	Lower 95%	Upper 95%	Mean TL (mm)	SE*	Lower 95%	Upper 95%
Experiment 1									
Hatchery	Chinook salmon	60	0.05	0.50	0.70	26.9	0.38	26.19	27.68
River									
Enhanced sites	Chinook salmon	29	0.03	0.24	0.35	25.2	0.12	24.77	25.55
Unenhanced sites	Chinook salmon	22	0.02	0.18	0.26	25.1	0.02	24.81	25.43
Experiment 2									
Hatchery	Chinook salmon	88	0.04	0.76	1.00	22.6	0.44	21.32	23.78
	Steelhead	84	0.08	0.62	1.00	22.2	0.19	21.69	22.73
River gravel	Chinook salmon	58	0.04	0.50	0.65	18.5	0.84	16.81	20.21
	Steelhead	61	0.03	0.54	0.68	19.0	0.89	17.20	20.79

*A pooled estimate of error variance was used.

and recorded. Surface samples were collected by pebble count at three randomly selected transects (~100 samples per transect) at each site using methods similar to those of Bauer and Burton (1993). Three 30-m longitudinal transects were randomly placed at each site. Surveyors collected substrate samples by hand every 0.3 m along the transect and used a round-holed template to measure size. Substrate from pebble counts was categorized into 12 sizes: <8.0, 8.0, 16.0, 22.2, 31.8, 44.5, 63.5, 89.0, 127.0, 177.8, 254.0, and > 254.0 mm. Categorization was based on the largest slot (round hole with specified diameter) through which an individual pebble could not be passed.

Intergravel permeability, DO, temperature, and turbidity

Intergravel water-quality measurements were taken at each site prior to egg-tube placement and immediately after egg-tube removal. A modified Terhune Mark VI standpipe was driven into the gravel to measure gravel permeability, DO, and water temperature following Barnard and McBain (1994). We collected water samples from the standpipe with a vacuum hand pump apparatus (Saiki and Martin 1996). Samples were taken at depths of 15, 30, and 45 cm to evaluate stratification of compaction and sedimentation within the known depth ranges of chinook salmon and steelhead spawning (Vronskiy 1972; Chapman 1988; Bjornn and Reiser 1991). Approximately 200 mL of water was collected from each sample and transported to the laboratory to measure turbidity in nephelometric turbidity units (NTU), total suspended solids (TSS), and volatile suspended solids (VSS). Turbidity was measured with a Hach 2100P turbidimeter. TSS samples were filtered through a 50-µm sieve, then passed through a precombusted gas fiber filter, dried to 60 °C, and weighed (American Public Health Association et al. 1995). Ambient DO and stream temperature (15 cm below the water surface) as well as intergravel DO and water temperature were recorded with a YSI 55 dissolved-oxygen meter. An Onset StowAway TidbiT temperature logger (–4 °C to +37 °C) was buried with the eighth tube (starting with top left tube No. 1) at each monitoring location (Fig. 2). Loggers recorded water temperature within the gravel every 60 min for the duration of the monitoring period (approximately 26 days). Hourly temperature data were totaled to calculate temperature-hours for each site.

Survival, development, and general condition

Based on observation of the hatchery control group, egg tubes were removed from the gravel when embryos reached the alevin stage and at least 10% showed capability of self-orientation in water current, typical of the swim-up stage. Live alevins were counted, measured for total length (TL), and assessed for anomalies (such as disease or deformities). Alevin mortalities and unhatched embryos were enumerated and recorded.

Data analyses

We used a one-way *t* test to compare mean survival rates and lengths of chinook salmon alevins buried in enhanced and unenhanced gravels (Zar 1999). To build a survival and growth model for chinook salmon and steelhead embryos, principal components analysis (PCA) was used to reduce the number of physical condition variables in the data set. This analysis was performed with SPSS® version 10 (SPSS Inc. 1997). We used the B4 selection method, as described in Joliffe (1972) and prescribed by Talmage et al. (2002), to select representative environmental variables indicated by the first four axes. We used multiple linear regression to build preliminary models with these independent variables to predict mean survival and mean TL of chinook salmon and steelhead alevins using the JMP linear regression model function, which performs an analysis of variance (ANOVA) (Sall et al. 2001). Alternate variables were then exchanged to strengthen the models. We also used ANOVA to compare the independent variables with alevin survival and TL. A significance level of 0.05 was used in statistical tests.

Results

Experiment 1: chinook salmon embryo survival and growth in enhanced and unenhanced spawning gravels

Chinook salmon embryos used to compare enhanced and unenhanced gravels were recovered on 8 January 2002, 28 days after egg-tube placement. Survival of chinook salmon

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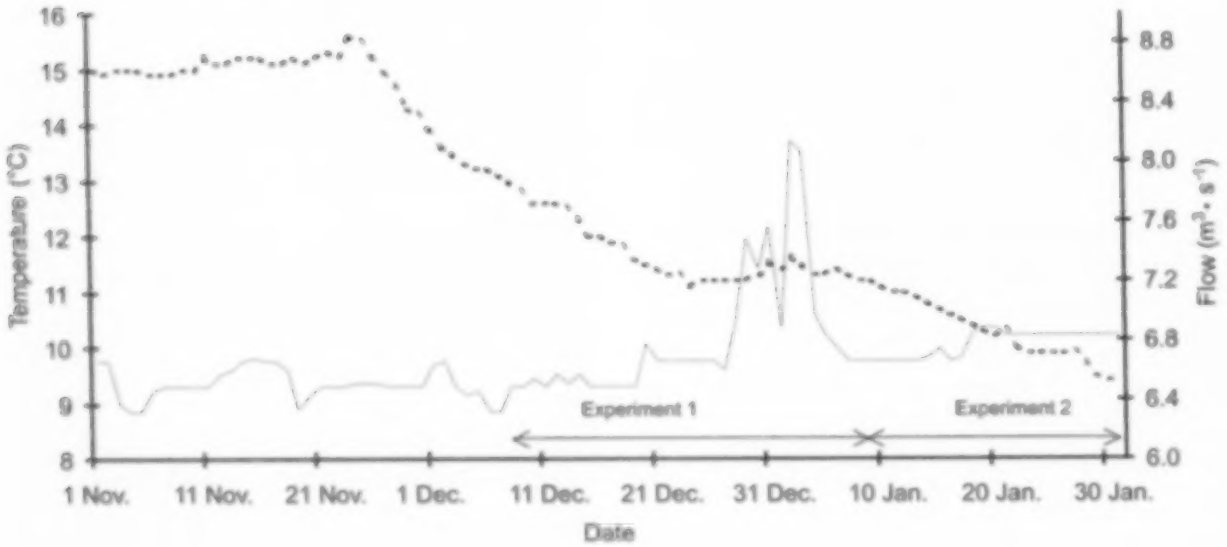
Table 2. Physical parameters associated with 10 egg tube monitoring sites and the Mokelumne River Fish Hatchery (control site)

					Peizometer measurements taken at time of egg-tube planting								
					Temperature (°C)			DO (ppm)			Permeability (mL·s^{-1})		
Site No.	DFCD[a] (km)	Water depth (m)	Stream velocity (m·s^{-1})	AT[a] (°C)	15 cm	30 cm	45 cm	15 cm	30 cm	45 cm	15 cm	30 cm	45 cm
Control	0.1			10.15	9.8			10.7			63.0		
1	0.8	0.3	0.65	10.10	9.8	10.0	10.2	10.2	7.7	6.1	38.0	41.0	28.0
2	1.4	0.2	0.78	9.97	9.6	10.0	10.0	9.9	9.5	9.1	42.0	17.5	9.3
3	1.7	0.2	0.67	9.79	10.3	9.8	9.8	9.2	6.9	5.9	40.5	14.0	25.0
4	1.8	0.2	0.75	9.88	10.6	10.1	9.9	8.0	8.2	8.5	41.5	19.0	16.5
5	2.3	0.2	0.75	10.11	10.1	10.0	9.7	10.3	10.1	10.1	35.5	9.3	5.5
6	6.3	0.2	0.89	9.73	9.8	9.9	9.8	9.3	8.5	6.9	44.9	43.6	32.5
7	7.1	0.2	0.65	9.79	9.9	9.5	9.5	9.6	7.3	6.4	44.8	42.5	35.5
8	8.5	0.4	0.96	9.87	9.5	9.5	9.6	9.2	6.4	6.1	44.1	23.9	8.5
9	9.5	0.3	1.02	9.61	9.4	9.1	9.2	9.2	7.3	7.1	47.6	12.5	1.2
10	10.5	0.3	0.65	9.72	8.7	8.7	8.9	9.0	8.1	7.2	18.2	21.5	11.5

Note: DFCD, distance from Camanche Dam; AT, average temperature in egg tubes at 15 cm; DO, dissolved oxygen; NTU, nephelometric turbidity

Fig. 3. Mean daily discharge rate and temperature of water released from Camanche Dam into the lower Mokelumne River from 1 November 2001 to 31 January 2002. The broken line indicates the temperature of the Camanche Dam release; the solid line indicates the rate of the Camanche Dam release.



embryos was highly variable. The chinook salmon embryo survival rate ranged from 0% in several unenhanced-gravel tubes to over 63% in tubes used as controls within the MRFH (Table 1).

Growth of chinook salmon was also variable. Chinook salmon embryos ranged from 11 to 31 mm TL in tubes incubated at the MRFH, while embryos incubated in river-gravel tubes ranged from 13 mm TL (site 3) to 30 mm TL (sites 4 and 5). Survival of chinook salmon alevins was significantly higher in enhanced gravel than in unenhanced gravel (Table 1; $t = 2.022$, df = 8, $P < 0.039$). No significant difference was observed for growth in enhanced and unenhanced gravel ($t = 0.038$, df = 8, $P = 0.485$).

Experiment 2: physical parameters associated with 10 spawning sites and their predictive power for salmonid survival and growth

Camanche Dam releases to the LMR ranged from 6.6 m^3·s^{-1} on 1 December 2001 to 6.8 m^3·s^{-1} on 31 January 2002, with a peak of 8.1 m^3·s^{-1} on 2 January 2002 (Fig. 3). Physical parameters associated with the spawning sites are provided (Table 2). Average daily temperature varied within the constructed redds. Although temperatures were somewhat consistent during experiment 1, during experiment 2, mean gravel temperature was inversely correlated with distance downstream of Camanche Dam (Fig. 4). Moreover, daily temperature variation was also greater downstream.

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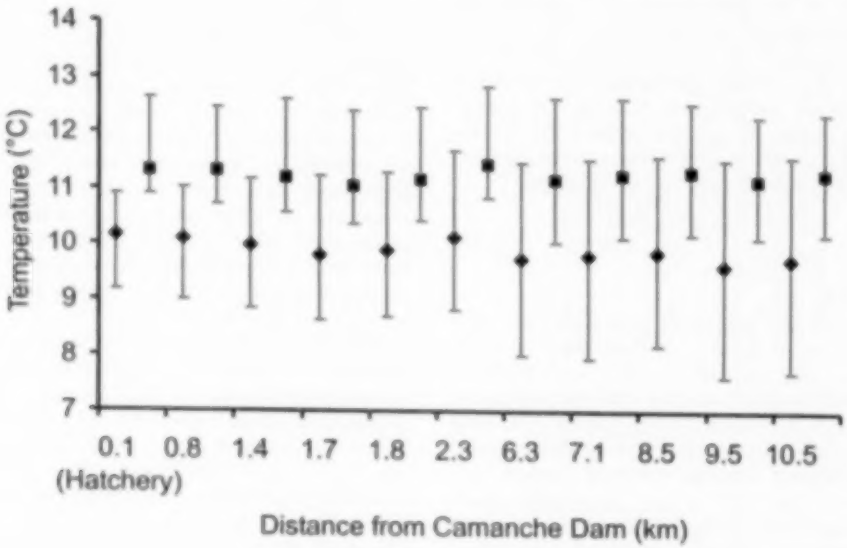
within the lower Mokelumne River, California, from 9 to 31 January 2002.

Turbidity (NTU)			TSS (mg·L^{-1})			VSS (mg·L^{-1})			d_{50} (mm)	
15 cm	30 cm	45 cm	15 cm	30 cm	45 cm	15 cm	30 cm	45 cm	Pebble count	Core
3.8			4.0			2.8				
24	1312	1024	14.6	362.4	809.7	6.3	61.8	122.4	385.6	370.5
970	1404	1328	297.2	547.8	573.3	30.1	59.2	73.9	423.3	455.5
24	1080	818	31.3	439.0	232.3	12.4	48.8	27.6	356.6	351.6
369	6137	4145	113.6	1150.7	1030.6	22.5	135.9	126.7	414.0	394.2
117	194	517	54.4	81.3	226.9	10.3	13.9	36.6	299.2	370.5
20	481	3050	32.3	365.6	1410.0	5.4	41.1	166.0	375.2	474.3
354	4450	3300	101.0	1504.7	465.7	18.8	175.3	57.3	203.7	159.2
18	369	374	55.1	226.1	577.0	6.3	25.8	67.9	251.5	314.6
343	378	1971	182.2	419.6	1194.0	28.6	48.9	95.0	203.4	74.1
696	1013	1180	177.0	377.6	471.1	25.0	46.8	59.5	152.2	156.7

units: TSS, total suspended solids; VSS, volatile suspended solids; d_{50}, median particle size.

Fig. 4. Temperatures recorded 15 cm below the gravel surface at 10 spawning sites and 15 cm below the water surface within the Mokelumne River Fish Hatchery (Hatchery). Average, minimum, and maximum hourly temperatures are shown for the monitoring period from 12 December 2001 through 8 January 2002 (experiment 1) (■) and for the monitoring period from 9 through 31 January 2002 (experiment 2) (◆).



Intergravel DO ranged from 6.1 mg·L^{-1} at 45 cm below the gravel surface to 10.11 mg·L^{-1} at 15 cm below the gravel surface. Intergravel permeability ranged from 1.2 mL·s^{-1} at 30 cm beneath the site 9 gravel surface to 48 mL·s^{-1} at 15 cm beneath the surface at the same site. We were able to draft 63 mL·s^{-1} through the standpipe in filtered hatchery water.

Spatial (i.e., distance from Camanche Dam) trends were observed in the variables collected (Table 3). As distance from Camanche Dam increased, average temperature within the gravels decreased and diurnal temperature fluctuations increased (Fig. 4). Surface substrate sizes, as indicated by pebble-count d_{50} (Pd_{50}) and general bed material size, as indicated by core-sample d_{50} (Cd_{50}), decreased as samples were taken farther from the dam. Correlations between turbidity, TSS, and VSS were strong, as were Cd_{50} and Pd_{50} measurements.

Chinook salmon and steelhead eggs used for the survival and growth models were recovered on 31 January 2002, 22 days after tube placement. Chinook salmon survival ranged from 0% to 100% in river gravel and from 74% to 98% within the MRFH. Similarly, steelhead survival ranged from 15% to 100% within river gravel and from 56% to 97% within the MRFH. Chinook salmon lengths ranged from 14 mm TL at site 5 to 25 mm TL within the tubes incubated at the MRFH. Steelhead lengths ranged from 13 mm TL at site 3 to 24 mm TL at all but two of the river sites. Chinook salmon and steelhead embryos tended to grow more slowly

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farther downstream from Camanche Dam, as indicated by average embryo size (Table 3).

While Cd_{50} and water depth appeared to have the strongest correlation with average rates of survival of chinook and steelhead embryos, respectively, no single physical parameter influenced both species strongly. The first four PCA axes explained over 87% of the total variance in physical conditions associated with the spawning locations (Table 4). The variables with the greatest loadings on each axis were distance from Camanche Dam, average VSS, and stream velocity.

Survival models

We used Cd_{50}, average VSS, and total temperature-hours as predictors of chinook salmon survival (Table 5A). The F ratio in the ANOVA for the overall model was significant at $F_{prob} < 0.01$ and the model accounted for 87% of the variation around the mean. We used average DO, temperature-hours, and average turbidity as predictors of steelhead survival (Table 5B). The F ratio in the ANOVA for the overall model was significant at $F_{prob} < 0.05$ and the model accounted for over 82% of the variation around the mean.

Growth models

We used temperature-hours, average permeability, average DO, and Cd_{50} as the independent variables to predict chinook salmon length at the time of egg-tube removal (Table 6A). The growth model accounted for 95% of the variation around the mean, with a significant F ratio for the ANOVA. We used Cd_{50}, average permeability, redd depth, and stream velocity as independent variables to predict steelhead length at the time of egg-tube removal (Table 6B). The growth model accounted for 89% of the variation around the mean, with a significant F ratio for the ANOVA.

Discussion

Growth and survival

Benefits documented for spawning salmonids and their developing embryos as a result of enhancement projects have been anecdotal, and typically inferred from measurements of physical habitat characteristics and observations of spawning activity (Zeh and Donni 1994; Van-Zyll-De-Jong et al. 1997). Our results indicate that LMR spawning gravel enhancements significantly increased chinook salmon embryo survival to swim-up stage up to 5 years after placement. Survival of salmonid embryos has been tied to DO (Coble 1961), temperature (Heming 1982), percent fines (Sear 1993), and permeability (Kondou et al. 2001) within spawning gravels. Merz and Setka (2004) showed that strategically placed gravel within the LMR significantly increased velocities and permeability, and decreased depths and fines, equilibrating the hyporheic and water-column environments, which supports our findings in this study. However, the short-term benefits of spawning-gravel enhancements may diminish through time if inter-annual bed mobilization from flushing flows is not provided (Wheaton 2003).

Although we observed no significant increase in embryonic growth in enhancement gravels during experiment 1, our preliminary egg-tube test showed a 24% average increase in survival and a 11% increase in growth of chinook salmon embryos placed in two enhanced sites when compared with two unenhanced sites in December 2000 (unpublished data). Embryo quality may have been a significant factor in the reduced benefits to growth observed in this study, considering that we observed 65%–100% survival in enhancement gravels in tubes buried for 4 weeks during our preliminary test and only 1%–67% within enhancement gravels during this study. Similar survival rates were also observed by hatchery staff monitoring the same egg lots incubated in the MRFH.

Physical correlations

The principal component correlations explain a few trends with respect to median grain sizes that are consistent with conventional geomorphic theory. First, surface bed material was consistently coarser than subsurface material. In gravel-bed streams, this is known as paving or armouring (Parker et al. 1982) and is thought to arise from differential erosion of coarse and fine grains in heterogeneous bed mixtures. Briefly, finer grains require less energy to erode than coarser grains, primarily because of their differences in mass. For example, a prolonged intermediate-flow event may produce hydraulic forces competent to erode fine- and medium-grained particles from the surface of a heterogeneous gravel bed, but not strong enough to erode the coarser grain particles. This, in turn, can lead to an armoured layer comprised of a higher percentage of coarse grains compared with a subsurface layer, which is not subjected to hydraulic forces adequate to winnow finer material away. Kondolf (1997) explains that, in regulated rivers like the LMR, surface armouring is often accentuated owing to flow-regulation conditions because larger particles that lag behind are less easily mobilized by hungry water below dams. Furthermore, dams block the passage of gravels, and once finer material (including spawning gravels) has winnowed away it is not replenished. Although the subsurface layers may provide a finite source of appropriately sized spawning gravels, they can become inaccessible or erodable under the protection of a coarse-armour veneer.

The second trend apparent in the principal component correlations is a reduction in grain size with distance downstream from Camanche Dam (fining). This fining of bed material is evident in both the surface median grain size and to a lesser extent the subsurface, consistent with the literature (e.g., Schumm and Stevens 1973; Ashworth and Ferguson 1989). Constantine et al. (2003) documented downstream fining in the gravel-bed reaches of the neighbouring Cosumnes River, but also noted the presence of a confined gravel-bed reach where downstream fining was not evident. They attributed the lack of decrease in grain size in that discrete reach to equal mobility of all bed material and incised channel morphologies that limit the freedom of the channel to migrate laterally. Given the incised nature of the LMR channel and the artificial reset of grain sizes at enhanced sites located throughout the LMR, one might suspect that the downstream fining trend would not persist in similarity to the Cosumnes River. However, the rather small percentage of the entire spawning reach actually covered by enhanced gravels (<2%) may prevent a noticeable influence on the general fining trend (Merz and Setka 2004). Furthermore, the equal mobility of all grain sizes observed in the Cosumnes River is in response to a nonregulated natural

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Table 3. Principal component correlations among dependent and independent variables for chinook salmon and steelhead embryos developing in spawning gravel of the lower Mokelumne River from 9 to 31 January 2002.

	Physical variable											
Variable	DFCD	WD	SV	TH	TA	PA	DOA	TURA	TSSA	VSSA	PD_{50}	Cd_{50}
Chinook salmon												
CSSurvival	–0.273	–0.302	0.353	0.063	0.339	–0.257	0.113	–0.373	–0.386	–0.449	0.487	0.635
CSAS	**–0.721**	–0.412	–0.090	0.681	0.554	–0.466	0.495	–0.170	–0.418	–0.320	0.685	0.690
CSSM	–0.661	–0.244	–0.405	**0.794**	0.408	–0.136	0.491	–0.464	–0.665	–0.493	0.546	**0.708**
CSSMX	–0.600	–0.173	–0.110	**0.788**	0.500	–0.249	0.411	–0.158	–0.385	–0.226	0.614	**0.731**
Steelhead												
STHSurvival	0.108	–0.625	–0.171	–0.142	–0.133	–0.302	0.386	0.505	0.298	0.215	–0.116	–0.099
STHAS	**–0.710**	–0.629	0.006	0.511	0.634	–0.182	0.549	–0.122	–0.262	–0.247	**0.781**	**0.831**
STHSM	0.381	0.325	0.246	–0.087	–0.343	0.101	0.237	0.216	0.451	0.441	–0.124	–0.037
STHMX	–0.535	–0.188	0.327	0.563	0.565	–0.309	0.544	–0.395	–0.428	–0.424	0.498	0.528
Physical variable												
WD	0.651											
SV	0.423	0.429										
TH	**–0.753**	–0.208	–0.385									
TA	**–0.883**	–0.209	–0.391	0.608								
PA	–0.103	–0.016	–0.149	–0.052	0.356							
DOA	–0.410	–0.408	–0.104	0.572	0.247	–0.372						
TURA	–0.122	–0.494	–0.258	–0.162	0.273	0.344	–0.078					
TSSA	0.132	–0.169	0.143	–0.433	0.091	0.487	–0.215	**0.836**				
VSSA	–0.360	–0.214	–0.078	–0.221	0.224	0.586	–0.183	**0.880**	0.954			
Pd_{50}	**–0.863**	–0.592	–0.104	0.524	**0.866**	0.240	0.289	0.178	0.107	0.220		
Cd_{50}	**–0.724**	–0.509	–0.089	0.579	**0.757**	0.214	0.380	–0.022	–0.127	–0.003	**0.891**	

Note: Boldface type denotes correlations greater than 0.7. CSSurvival, average chinook salmon survival rate; CSAS, chinook salmon average size; CSSM, chinook salmon minimum size; CSSMX, chinook salmon maximum size; STHSurvival, average steelhead survival rate; STHAS, steelhead average size; STHSM, steelhead minimum size; STHMX, steelhead maximum size; WD, water depth; SV, stream velocity; DFCD, distance from Camanche Dam; TH, temperature-hours; TA, average temperature within gravel; PA, average gravel permeability; DOA, average dissolved oxygen content within gravel; TURA, average water turbidity within gravel; TSSA, average total suspended solids within gravel; VSSA, average volatile suspended solids within gravel; Pd_{50}, pebble-count d_{50}; Cd_{50}, core-sample d_{50}.

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Table 4. Principal component loadings for the first four axes for physical conditions associated with 10 spawning sites within the lower Mokelumne River.

Characteristic	Axis 1	Axis 2	Axis 3	Axis 4
Distance from Camanche Dam	**–0.9280**	–0.1830	–0.0372	0.0344
Average ambient temperature	0.8790	–0.2220	0.0037	–0.2330
Temperature-hours	0.8780	–0.2210	0.0093	–0.2340
Core-sample d_{50}	0.8110	0.1470	0.4170	0.1830
Pebble-count d_{50}	0.7950	0.3620	0.3660	0.2090
Average dissolved oxygen concn.	0.6190	–0.1980	–0.3420	0.4270
Water depth	–0.5930	–0.4490	0.3800	–0.2980
Average volatile suspended solids	–0.1180	**0.9490**	–0.0025	–0.0313
Average total suspended solids	–0.3020	0.9060	0.0128	0.1710
Average turbidity	–0.0134	0.9030	–0.3450	0.0386
Average permeability	–0.0040	0.6330	0.4700	–0.4860
Stream velocity	–0.4250	–0.1610	**0.5580**	**0.6270**
Percent total variance explained	39.30	29.05	10.19	9.33

Note: Values in boldface type indicate the component with the highest loading on each axis.

Table 5. Statistics and associated multiple regression results for two models used to predict (A) chinook salmon and (B) steelhead embryo survival in Mokelumne River spawning gravel.

(A) Chinook salmon.					
Summary of fit	R^2	R^2 adj.	Root mean square error	Mean of response	Sum of weights
	0.8650	0.7975	0.0807	0.5723	10
Source	df	Sum of squares	Mean square	F ratio	Prob > F
Model	3	0.2503	0.0834	12.8116	0.0051
Error	6	0.0391	0.0065		
Corrected total	9	0.2893			
Effect tests	N_{param}	df	Sum of squares	F ratio	Prob > F
Core-sample d_{50}	1	1	0.1917	29.4346	0.0016
Average VSS	1	1	0.0934	14.3472	0.0091
Temperature-hours	1	1	0.0760	11.6651	0.0142
(B) Steelhead.					
Summary of fit	R^2	R^2 adj.	Root mean square error	Mean of response	Sum of weights
	0.8232	0.6818	0.0717	0.6139	10
Source	df	Sum of squares	Mean square	F Ratio	Prob > F
Model	4	0.1196	0.0299	5.8201	0.0402
Error	5	0.0257	0.0051		
Corrected total	9	0.1453			
Effect tests	N_{param}	df	Sum of squares	F ratio	Prob > F
Average DO	1	1	0.0373	7.2675	0.0430
Temperature-hours	1	1	0.0356	6.9339	0.0464
Average turbidity	1	1	0.0361	7.0257	0.0454
Average permeability	1	1	0.0072	1.4078	0.2887

Note: N_{param}, number of parameters; adj., adjusted.

flow regime with no major dams blocking the replenishment of sediment. Thus, the armoured surface substrates of the LMR may exhibit downstream fining through the coarse relic deposits left behind from the pre-regulation flow and sediment regime.

We also observed a strong correlation between water temperature and distance downstream from Camanche Dam, evident in both average temperature and temperature-hours. Preece and Jones (2002) observed a 3-week lag in and a 5.0 °C reduction of annual maximum daily temperature on Australia's Namoi River after construction of a dam. Similarly, Camanche Reservoir acts as an insulator, cooling water within the spawning reaches of the LMR during summer and fall. However, this pattern is reversed during the winter period, with water actually cooling farther downstream from the dam.

Correlations between physical and biological parameters

Substrate-size Cd_{50} was significantly correlated with chinook salmon survival and, along with temperature-hours and

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Table 6. Statistics and associated multiple regression results for two models used to predict chinook salmon (A) and steelhead (B) growth in Mokelumne River spawning gravel.

(A) Chinook salmon.					
Summary of fit	R^2	R^2 adj.	Root mean square error	Mean of response	Sum of weights
	0.9472	0.9050	0.3162	20.6088	10
Source	df	Sum of squares	Mean square	F ratio	Prob > F
Model	4	8.9686	2.2422	22.4320	0.0022
Error	5	0.4998	0.1000		
Corrected total	9	9.4684			
Effect tests	N_{param}	df	Sum of squares	F ratio	Prob > F
Temperature hours	1	1	0.6773	6.7766	0.0481
Average permeability	1	1	3.2321	32.3358	0.0023
Average dissolved oxygen	1	1	0.3008	3.0094	0.1433
Core d_{50}	1	1	2.7874	27.8869	0.0032
(B) Steelhead.					
Summary of fit	R^2	R^2 adj.	Root mean square error	Mean of response	Sum of weights
	0.8857	0.7943	0.1825	21.1139	10
Source	df	Sum of squares	Mean square	F ratio	Prob > F
Model	4	1.2910	0.3228	9.6898	0.0142
Error	5	0.1665	0.0333		
Corrected total	9	1.4576			
Effect tests	N_{param}	df	Sum of squares	F ratio	Prob > F
Core d_{50}	1	1	0.5481	16.4557	0.0098
Average permeability	1	1	0.1379	4.1391	0.0976
Depth	1	1	0.0859	2.5776	0.1693
Velocity	1	1	0.0294	0.8815	0.3909

Note: N_{param}, number of parameters; adj., adjusted.

VSS, explained 86% of the variability in predicted survival. Likewise, growth regression equations for both chinook and steelhead included Cd_{50}. The mechanistic pathway of the Cd_{50} effect likely involved a relationship with permeability (Sowden and Power 1985). Interestingly, while we observed strong correlations between Cd_{50} chinook alevin survival and growth, Cd_{50} only appeared to be strongly correlated with steelhead growth, not survival. According to Chapman (1988), mean particle size is not as good an indicator of steelhead survival as for other salmonid species. Usefulness of mean particle size may be limited because gravel mixtures with the same geometric mean can have different size compositions. While our study design focused on survival of salmonid embryos within the hyporheic environment, the placement of eggs in a tube provided protection from physical impacts from all but the smallest substrates (<2.9 mm diameter). It is expected that Cd_{50} would have a direct egg-size-dependent effect on survival of eggs deposited directly in substrate. Likely, direct impacts related to substrate size include physical abrasion and crushing in the case of smaller gravel and interstitial space or, in the case of larger interstitial space, increased trauma due to currents and decreased cushioning. In a similar vein, egg size varies between salmonid species and even within species. Fecundity and egg size are inversely related in Pacific salmon and vary over latitudinal clines, with northernmost populations producing more but smaller eggs (Flemming and Gross 1990). Quinn et al. (1995) showed that there was a correlation between egg and substrate size for sockeye salmon (*Oncorhynchus nerka*), implying a selective effect of gravel size on egg size. Natural-selection effects on salmonid egg size can occur over decades and may be influenced by hatchery production (Kinnison et al. 1998). Independent of body size, there is little variation in egg size within populations of salmonids and we assumed that the egg sizes in our study were similar for each species for each experiment (Flemming and Gross 1990).

Development rates in sockeye and chinook salmon embryos are optimized for thermal regimes present within a given population's home spawning area, suggesting a genetic component that may vary between populations (Hendry et al. 1998; Kinnison et al. 1998). Although we used Feather River steelhead eggs, we assume that there is little difference between the present populations considering the high egg-importation rate by hatcheries over the past four decades (Bryant 2000). Even so, genetic influence on development rates should be considered when compiling information on restoration techniques and resulting salmonid physiological performance (growth, behaviour, mortality).

Intra-watershed variation must also be considered. For instance, the thermal shift in the LMR below Camanche Dam appears to affect embryo survival and growth. We observed both slower growth with cooling downstream of the dam late in the season and increased growth with warming earlier in

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the season (unpublished data). The reservoir insulating effect (i.e., warming water in winter and cooling water in summer and fall) will affect oxygen-saturation levels as well.

Numerous studies have documented correlations between individual physical parameters and embryo survival (Coble 1961; Heming 1982; Sear 1993). However, a specific action, such as increasing substrate permeability, may also influence temperature, DO, or even predator access to developing embryos. Shepherd et al. (1986) showed that the thermal mass of the substrate in Pacific Northwest coastal streams caused parallel but lagged and buffered heating and cooling trends in infiltration-source intergravel water compared with surface water. Similarly, this study and other work performed on LMR spawning gravel enhancement demonstrated that during the early portion of the fall-run chinook salmon spawning season (October through early November), intergravel water may be as much as 2.3 °C warmer than surface water, potentially influencing growth and development within the different embryo life stages. Salmonid egg to fry development is generally partitioned into three phases: prehatch, posthatch, and terminal phase. During the posthatch phase, yolk utilization increases markedly concurrently with increased somatic growth and organogenesis. The terminal phase is when the fish begins the transfer to exogenous feeding. It is during the terminal phase that suboptimal environmental conditions effects are manifested in either reduced physiological performance or increased mortality. Prior to the terminal phase suboptimal conditions generally affect growth rates and yolk-utilization efficiencies, whereas sublethal or critical conditions lead to developmental arrest and death. Progression of embryonic development is highly susceptible to regulation by extraneous factors such as temperature and DO, both of which are correlated with hyporheic flow (Chapman 1988). During the study period intergravel temperatures ranged from 7.6 to 12.8 °C, well within the optimal incubation range for chinook salmon and steelhead (Bjornn and Reiser 1991). Results from experiment 2 indicate that, as expected, temperature affected the growth and presumably the yolk-utilization efficiency of the embryos, but had no significant impact on survival. However, this study was performed during the middle of the LMR redd incubation period (October through April) and results could be different at either end of this period.

The use of several physical-parameter measurements to construct a predictive model of chinook salmon and steelhead survival and growth worked well. In addition to the parameters discussed above, VSS, DO, permeability, depth, and water velocities were all used in regression equations to predict growth and survival. While literature and previous work on the LMR support the fact that each of the parameters listed can influence salmonid physiology, their inclusion in our predictive model is not necessarily indicative of a significant effect individually (Garric et al. 1990). In our analysis we found that there were significant differences in the predictive power of regression equations based on what combination of parameters was used. While individually some parameters, such as average temperature, had a higher correlation with average steelhead size, when included in a suite of parameters they were not as useful as stream velocity in maximizing the predictive power of the regression equation. While the bulk of variation in growth and survival is explained by two or three parameters, the inclusion of minimally correlated measures may act to fine-tune equations to particular sites or systems. Leftwich et al. (1997) compared the predictive power of local and regional habitat models for the tangerine darter (*Percina aurantiaca*). Their results indicate significant differences in the relative importance of limiting factors between habitats, which limited the transferability of local-habitat models. It is likely that the influence of nonlimiting parameters in predictive models would also vary geographically, emphasizing the importance of collecting a full suite of data when evaluating restoration projects and the significant relatedness between some parameters (Koslow et al. 2002).

Management implications

It is important to note that the steelhead and chinook salmon embryos were not exposed to the test environment during their earliest development period. Even so, our results suggest that survival and development effects from manipulation of the spawning and incubation environment can be accurately measured. By increasing substrate porosity, hyporheic and surface water quality can be equilibrated. However, these synergistic effects greatly complicate evaluation of enhancement benefits, especially when parameters are assessed individually. These effects may explain documented low correlations between alevin survival and substrate-permeability measurements.

The simple test comparing embryo survival in enhanced and unenhanced gravels performed here provides some of the first evidence of short-term biological benefits of spawning-habitat rehabilitation. From a subset of the 12 parameters we were able to develop predictive multiple regression models for chinook salmon and steelhead embryo survival and growth, which suggests that benefits from gravel augmentation can be predicted and measured. However, this is not to suggest that all forms of spawning-habitat rehabilitation will or should yield similar improvements in embryo survival. Instead, there are logical explanations for differences between substrate conditions in enhanced and unenhanced gravels that may then explain the observed differences in survivability. The four spawning bed enhancement sites consisted of riffles constructed between 1994 and 2001. Unlike gravel augmentation or hydraulic structure placement forms of rehabilitation, these projects involve the direct placement of clean, optimally sized spawning gravels to form immediate spawning habitat (Wheaton 2003). On the LMR, typical fill depths of these projects are greater than egg-burial depths (>25 cm). Merz and Setka (2004) showed significant reductions in channel depth, sediment fines, and intergravel temperature and significant increases in stream velocities, intergravel permeability, and DO. Therefore, strategic gravel placement equilibrated the hyporheic and water-column environments and related positively to embryo survival rates. As Pasternack et al. (2004) point out, ad hoc implementation (as done on the LMR from 1991 to 2000) of spawning bed enhancement projects without a systematic design process (e.g., Wheaton 2003) can lead to less efficient gravel placement. To better gauge the benefits of such projects to the effort applied, we suggest appropriate cost-benefit analysis of material and effort in terms of actual embryo or fry production. Furthermore, while site-specific

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augmentation appears promising, it is important to note that the LMR is a relatively low gradient stream with a highly regulated flow. Using the methods presented here in other river systems should increase our understanding of how gravel-enhancement projects work in different situations. This understanding, in turn, can be linked to the establishment of healthy ecosystem, hydrologic, and geomorphic processes.

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Effects of catchment characteristics and disturbances on storage and export of dissolved organic carbon in a boreal headwater stream

Graham R. Hillman, Joseph C. Feng, Cecilia C. Feng, and Yonghe Wang

Abstract: The transportation of large amounts of dissolved organic carbon (DOC) down a stream within a 15.51-km^2 catchment in Alberta, Canada, related directly to events, such as high rainfall and beaver (*Castor canadensis*) dam failures, that created major disturbances. A 2.3-km section of the stream was drastically altered in June 1994 when a flood wave resulting from a breached beaver dam deposited large amounts of debris and sediment within the section. Results from stream DOC-storage analyses, in which a difference method was used, suggest that the organic-debris dams created by the failed dam event served as both sources and sinks for DOC. Discharge and DOC measurements at hydrometric stations located at intervals along the stream indicated that storage of DOC on the catchment was strongly influenced by the presence of wetlands and beaver. In 1994 and 1995, disturbances occurring during periods totalling 17 days and 28 days accounted for 94% (1374 kg·km^{-2}) and 84% (204 kg·km^{-2}), respectively, of the amount of DOC exported from the catchment. DOC concentrations in the stream were greatest (77.0 mg·L^{-1}) near the top of the catchment and decreased progressively downstream to the catchment outlet, where the mean concentration was 23.3 mg·L^{-1}.

Résumé : Le transport de grandes quantités de matière organique dissoute (DOC) vers aval dans un cours d'eau ayant un bassin versant de 15,51 km^2 en Alberta, Canada, est relié directement à des événements, tels que des précipitations abondantes ou des ruptures de barrages de castors (*Castor canadensis*), qui causent des perturbations majeures. Une section de 2,3 km du cours d'eau a été altérée de façon catastrophique en juin 1994 lorsqu'une onde de crue provenant de la rupture d'un barrage de castors a déposé de grandes quantités de débris et de sédiments dans la section. Des analyses d'accumulation de DOC dans le cours d'eau, basées sur une méthode de différence, indiquent que les barrages de débris organiques créés par la rupture du barrage de castors servent à la fois de sources et de drains de DOC. Les mesures de débit et de DOC faites à des stations hydrométriques situées à intervalles le long du cours d'eau indiquent que l'accumulation de DOC dans le bassin versant est fortement influencée par la présence de terres humides et de castors. En 1994 et 1995, les perturbations qui ont duré respectivement en tout 17 et 28 jours ont été responsables de 94 % (1374 kg·km^{-2}) et 84 % (204 kg·km^{-2}) de la quantité de DOC exportée du bassin versant. Les concentrations de DOC dans le cours d'eau étaient maximales (77,0 mg·L^{-1}) près de l'amont du bassin versant et elles ont décru progressivement vers l'aval jusqu'à l'embouchure où la concentration moyenne était de 23,3 mg·L^{-1}.

[Traduit par la Rédaction]

Introduction

Small headwater stream ecosystems are commonly the source of coarse particulate organic matter that is broken down within the small stream systems into progressively smaller size fractions that provide significant input to the energy budget and food web of aquatic ecosystems (Dahm 1981; Meyer et al. 1988). Thus it is important to retain coarse particulate organic matter within the headwater regions. Organic-debris dams, which are accumulations of organic matter extending partially or completely across stream channels, are important retention mechanisms of coarse particulate organic matter in forested areas with rocky substrates (Bilby and Likens 1980; Bilby 1981). Dissolved organic matter, the dissolved component of decomposed coarse particulate organic matter, is frequently measured as dissolved organic carbon (DOC) (Kaplan et al. 1980; Bourbonniere 1989; Evans et al. 1989). DOC in water is derived from leached plant material and its concentration is controlled by a combination of primary production of plant matter and decomposition rates (Thurman 1985). Wetlands such as bogs, swamps, and fens, where there is a large net primary production of emergent plants, are a prominent feature of the boreal landscape. Streams draining wetlands are characteristically brown and slow moving. The long-term color is strongly correlated with long-term DOC concentra-

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tions in streams and lakes (Molot and Dillon 1997). Thus streams draining catchments with substantial areas of wetlands contain higher DOC concentrations than streams draining catchments where wetlands are absent or form only a small portion of the total area (Thurman 1985; Eckhardt and Moore 1990; Koprivnjak and Moore 1992).

In the boreal forest, beaver (*Castor canadensis*) are abundant and exert a significant influence on stream hydrology and DOC. In Quebec, DOC export from catchments where beaver activity was most intense was considerably higher than that from catchments where there was no beaver activity (Naiman 1982; Naiman et al. 1986). Beaver concentrate organic materials (coarse particulate organic matter) in and adjacent to streams through their tree-cutting, food-gathering, and dam- and lodge-building activities. These activities generally result in higher DOC concentrations downstream than upstream from such activities (Smith et al. 1991). Conversely, a catastrophic beaver-dam failure results in a rapid flushing of materials that may have significant short-term effects on downstream insect densities and fish communities (Stock and Schlosser 1991).

Natural or anthropogenic disturbances may affect aquatic ecosystems by altering light penetration, pH, dissolved oxygen concentration, water temperature, energy pools, available food sources sustaining aquatic biota, and the concentrations of chemical constituents (dissolved organic matter, nutrients, and other elements). The impact of some disturbances, such as careful forestry practices, on most water-quality variables is predictable and tends to be minimal (Binkley and Brown 1993), but their effects on carbon are much more variable (Hope et al. 1994). The effects of forestry and other land-use practices such as burning, acidification, and drainage on DOC dynamics are summarized in Hope et al. (1994).

This study is the outcome of an experiment that began as an investigation of the effects of extensive timber harvesting in the boreal forest on stream hydrology and water quality. A 15.51-km^2 catchment was instrumented in 1993 and timber-harvested in winter 1993–1994. On 8 June 1994, the catchment's main channel (Rocky Creek) sustained a major disturbance when a beaver dam burst and the resulting flood wave demolished 50% of the instrumentation (Hillman 1998). Because the impact of this event on water quality far exceeded any effects that timber harvesting might have, the study was modified to consider the effects of total disturbance, rather than the effects of timber harvesting alone, on water quality.

Where beaver are active, dam failures are probably very common but go largely unnoticed because beaver habitat is usually remote from human habitation. Furthermore, beaver are quick to repair the damaged structures. On Wolverine Creek, which drains the 9.84-km^2 catchment adjacent to that of Rocky Creek, catastrophic dam failures resulted in peak discharges of 34.0 and 22.9 m^3·s^{-1} in June 1968 and July 1969, respectively. These flash floods washed out the road downstream from the stream gauge. Invariably, a catastrophic dam failure will create a domino effect when the water released destroys other dams downstream. Catastrophic dam failures and flash floods also occur when heavy equipment or explosives are used to remove beaver dams. Butler (1995) has provided a review of beaver-dam failures and their effects.

In this study, we hypothesized that changes in DOC concentrations and fluxes along the stream are related to characteristics of the catchments and stream channels they drain. We further hypothesized that DOC export is dependent not only on specific discharge events but also on antecedent conditions, and that major disturbances such as the breaching of beaver dams dominate export and have a profound effect on post-disturbance conditions.

Material and methods

Study area

The study was conducted on Rocky Creek (54°56′N, 117°46′W), which drains a 15.51-km^2 catchment located about 35 km southwest of Valleyview, Alberta, in the headwaters of the Peace River (Fig. 1). At Valleyview, the mean annual temperature is 2.3 °C and the average January and July temperatures are –15.9 and 15.8 °C, respectively (Atmospheric Environment Service 1982*a*). The average annual precipitation is 519 mm, 58% of which falls in May through September; winter snowfall is 33% of annual precipitation (Atmospheric Environment Service 1982*b*). The precipitation record indicates that high-rainfall events, in the 40–100 mm range, can be expected 1–3 times during the period May–October. Long-term (1967–1987) discharge records for Rocky Creek show that 60%–70% of the annual streamflow occurs in March through May as snowmelt runoff, 28%–38% runs off during June through September, and the remainder occurs through the winter months. The mean annual water yield from Rocky Creek for the period 1967–1987 was 0.934×10^6 m^3 (60 mm).

The catchment, located in the Central Mixedwood Subregion of the Boreal Forest Natural Region (Alberta Environmental Protection 1994), is underlain by horizontally bedded sandstone, siltstone, and shale. Above this is till mantled by a variable thickness of stony glaciolacustrine deposits on which the dominant soils have surface textures ranging from clay-loam to sandy-loam (Martz 1978). Organic soils are concentrated in the 2-km^2 poor fen (Zoltai 1988) south of the lake and in the 0.90-km^2 wetland near the centre of the catchment (Fig. 1). Aspen (*Populus tremuloides* Michx.) is the dominant tree species in the catchment, but white spruce (*Picea glauca* (Moench) Voss is also present. On organic soils, black spruce (*Picea mariana* (Mill.) BSP) and to a lesser extent, tamarack (*Larix laricina* (Du Roi) K. Koch) is dominant.

Beaver activities have a significant impact on the ecology and stream hydrology of Rocky Creek and adjacent catchments. Numerous dams and ponds are scattered throughout the riparian areas and wetlands and along the stream channels. The flood wave arising from the beaver-dam burst on Rocky Creek (at point A in Fig. 1) created a chain reaction by breaching all the beaver dams downstream to point B, adding the force of water released to that of the initial flood wave. During the study period there were five beaver dams between hydrometric/water-sampling stations 1 and 2, two dams between stations 3 and 4, six dams in the wetland between stations 6 and 8, and four dams between stations 8 and 9 (Fig. 1). Four ponds between stations 1 and 2 were contiguous in a stepwise pattern, as were two of the ponds

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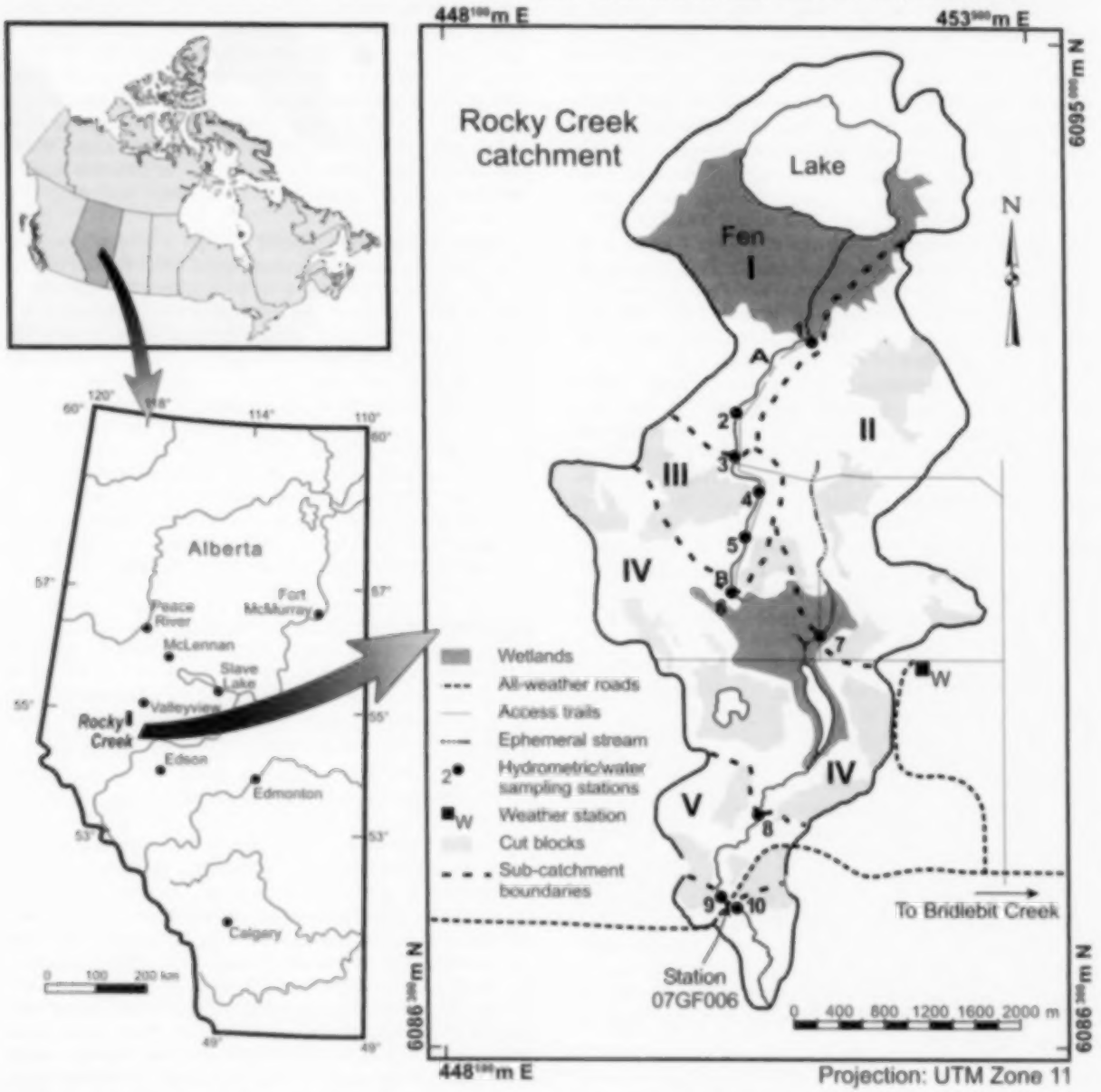
Fig. 1. Location of the Rocky Creek catchment in Alberta, Canada, showing contributing areas (or subcatchments; denoted by roman numerals), cut blocks, instrumentation, and wetlands. Station 07GF006 is part of the Alberta Sustainable Development stream-gauging network. The flood wave resulting from the dam failure had the greatest impact on the stream channel between points A and B.



between stations 8 and 9. Beaver eventually restored some of the dams destroyed by the flood between stations 1 and 3.

Prior to timber harvesting in winter 1993–1994, when 21% of the Rocky Creek catchment area was clear-cut in patches (0.03–0.47 km^2), beaver cuttings and 5 m wide seismic lines cleared for oil- and gas-exploration purposes were the only other significant vegetation disturbances. Buffer strips 150 m wide protected watercourses, riparian areas, and wetlands during timber-harvesting operations. The harvesting operation played no part in initiating the dam failure because all the cut blocks are located downslope from the dam (Fig. 1). We assume that in the absence of intense rainfall at the time of dam failure, the dam was weakened or undermined by muskrats (*Ondatra zibethicus*). These animals were believed to have caused similar dam failures on Wolverine Creek in the catchment adjacent to that of Rocky Creek, because their tunnels were visible at the base of one failed dam (Hillman 1998).

Sampling stations

Ten hydrometric/water-sampling stations were established on Rocky Creek (Fig. 1). Stations 9 and 10 were located

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close together, upstream and downstream, respectively, from the road crossing. Water-level-recording systems were installed at stations 1 (1994), 3 (1993), 6 (1993), 7 (1994), and 8 (1994). Because stations 2 and 3 were close together, it was assumed that discharges at the two stations were the same. Similarly, discharges at stations 4 and 5 were assumed to be the same as at station 6. Discharges at stations 9 and 10 were assumed to be the same as at station 07GF006.

Each station, with the exception of 07GF006, recorded water levels in Lakewood Systems Ultra-loggers every 3 h; station 07GF006 recorded hourly measurements at a 90° sharp-crested v-notch weir. Stage–discharge relationships were established for stations 3, 6, 7, 8, and 07GF006. It was not possible to measure discharge at station 1 because the flow there was usually too diffuse and the flow velocity too low. Stream-discharge measurements were first obtained from all five stations simultaneously on 16 July 1994. Precipitation data were obtained from the weather station located outside the east boundary of the catchment (Fig. 1).

To trace the contributions and withdrawals of DOC from its different parts, the catchment was divided into five areas or subcatchments, the exit points of which coincided with the station locations where stream discharge was measured (Fig. 1). Areas I (5.31 km^2) and II (4.11 km^2) are located upstream from stations 3 and 7, respectively. Area III (1.11 km^2) drains into the channel between stations 3 and 6, and area IV (4.07 km^2) consists of the most westerly portion of the catchment combined with the wetland located downstream from stations 6 and 7 and upstream from station 8. Area V (0.92 km^2) is the area drained by Rocky Creek between stations 8 and 9.

Total exports of DOC from the catchment were measured at station 07GF006. Outflows of DOC past station 3 became inflows into the channel of area III (Fig. 1). Similarly, outflows of DOC past stations 6 and 7 became inflows into the channel of area IV. In this paper, the daily change in storage of DOC (ΔS) for each channel section is defined as the difference between the daily outflow and inflow of DOC. A positive ΔS value indicates that more DOC left a channel section than entered it. Conversely, a negative ΔS value signifies storage of DOC in the channel section. Therefore, the sum of the ΔS values for all channel sections is equal to the amount of DOC exported from the Rocky Creek catchment on a particular day. The daily change in storage for the channel sections in areas I and II was always positive (except when $Q = 0$ $m^3 \cdot s^{-1}$) because it was assumed that no influx of DOC occurred from beyond the boundaries of this region of the upper catchment.

Water sampling and DOC analyses

In 1993, grab sampling for DOC at each station started on 30 June, but most samples were collected in August and September, after the American Sigma Streamline 800SL portable samplers were installed. In 1994, stream water was sampled twice a day, at noon and midnight, from mid-May till the end of September, nearly uninterrupted, except for the 10 days following the beaver-dam burst. In 1995, water samples were collected once every 2 days starting in early May and continuing until the beginning of October. DOC concentrations for the alternate days when samples were not collected were estimated by taking the average of the concentrations determined on the previous and following days.

Samples were obtained periodically from soil-water seepage and groundwater in piezometers and water level observation wells. The piezometers were located in groups of three oriented down the east slope perpendicular to Rocky Creek at stations 3, 4, and 5. One piezometer in each group was installed near the stream channel to a depth of 1.9–2.9 m, the second (3.8–6.6 m deep) at a midslope position, and the third (6.2–8.7 m deep) at the top of the slope. Water-level wells were installed near station 9 in a similar manner, but they included shallow (5–11 m deep) and deep (34–61 m) wells.

Water samples were filtered through a 0.5-µm glass-fibre filter. An automated Dohrmann Model DC-190 total organic carbon analyzer equipped with an autosampler was used to analyze DOC in water. The instrument was calibrated with a series of 1 to 100-mg·L^{-1} carbon standard solutions of potassium hydrogen phthalate. A 50-mg·L^{-1} carbon standard solution was analyzed 4 times and the mean signal response stored in the analyzer. A 5-mL aliquot of filtered-water sample was transferred into an autosampler vial and injected into the analyzer. Signals generated from the carbon content of water samples were calculated and converted into milligrams per litre carbon concentration automatically by the analyzer for comparison with that of the 50-mg·L^{-1} carbon standard. Four analyses per water sample were performed and their mean and standard deviation recorded.

Hypotheses and statistical analyses

We postulated that timber harvesting, wetlands, and beaver activities together on the Rocky Creek catchment had no significant effects on stream-water DOC concentrations. To verify our assumptions, we used the following general linear model to test the null hypothesis ($\alpha = 0.05$):

$$(1) \qquad DOC_{ijk} = \mu + SITE_i + YR_j + \beta t + \varepsilon_{ijk}$$

In the model, DOC_{ijk} is the daily DOC concentration, μ is the grand mean, $SITE_i$ represents the site effect ($i = 1, 2, \ldots, 10$); YR_j is the year's effect ($j = 1, 2, 3$ for 1993, 1994, and 1995), and ε_{ijk} is the error term; variable t is a covariate, and was defined as the time span between 1 January 1993 and the day when the observations were taken. The purpose of the linear combination βt was to measure the effect of covariate term t on the concentration. There would be no time effect if $\beta = 0$. The model was used to test both daily mean DOC and daily median DOC concentrations. The normality assumption of the error term in the model was tested using (*i*) all residuals, (*ii*) residuals on a site basis, (*iii*) residuals on a year basis, and (*iv*) residuals for all possible site–year combinations. For most tests, the normality assumption seemed not to hold, i.e., the residuals were not normally distributed. The shapes of the histogram plots for all residuals, however, were close to normally distributed but skewed to the right. The means were compared using the Bonferroni (Dunn) t test. Regression analyses were completed to determine if there was a significant correlation between DOC concentrations and stream discharge and between DOC concentrations and the area of wetlands in the catchment.

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Results and discussion

Data pooling

Significant differences in DOC concentration existed among years ($p < 0.001$) and among stations ($p < 0.001$), but day of the year had no significant effect ($p = 0.643$) on DOC concentration. The mean DOC concentration for 1994 (40.2 mg·L^{-1}) was significantly higher than those for 1993 (34.5 mg·L^{-1}) and 1995 (34.8 mg·L^{-1}), with no significant difference between those for 1993 and 1995. The greater DOC concentrations in 1994 were attributed to the high DOC concentrations (51.2–125.6 mg·L^{-1}) recorded at station 1 and the effects of the beaver-dam failure.

The mean station DOC concentrations can be divided into six separate groups, stations 1, 2, 3, and 7 being significantly different from each other and from all other stations (Table 1). There were no signification differences in DOC concentration among stations 4, 5, and 6, nor among stations 8, 9, and 10. The grouping together of stations 9 (upstream from the road crossing) and 10 (downstream from the crossing) indicates that the road crossing had no significant effects on DOC concentrations.

Subsequently, DOC-concentration data for stations in the same group were pooled to compute DOC fluxes. Thus, data for stations 4, 5, and 6 were combined, as were concentrations for stations 9 and 10. Data for station 8 were not pooled with those for stations 9 and 10 because the discharge at station 8 was usually different from that at the other two stations. In the following discussion, the pooled data for stations 4, 5, and 6 will be referred to as station 6 data and the combined data for stations 9 and 10 as station 9 data.

DOC fluxes

The mean daily DOC fluxes at different locations on Rocky Creek varied considerably during 1994–1995, the peak fluxes usually occurring during periods of high precipitation and increasing stream discharge (Fig. 2). At station 9, mean daily DOC fluxes peaked at 1274, 3426, and 2676 kg·day^{-1} on 9 June, 15 June, and 4 July 1994, respectively (Fig. 2*b*). These maxima are equivalent to exports from Rocky Creek of 82, 221, and 173 kg·km^{-2}·day^{-1}. Station 9 was the only station to be monitored during this hydrologically active period. Although most of the instrumentation was recording data by 31 May 1994, five of the stations were destroyed in the flood resulting from the beaver-dam failure on 8 June 1994. The hydrometric network was not restored to full operating condition until 16 July 1994, thus the period between 8 June and 16 July 1994 represents a sizeable gap in a critical section of the Rocky Creek discharge record. DOC sampling, however, recommenced at all stations on 15 June 1994.

The first peak (1274 kg·day^{-1} at station 9) is associated with the beaver-dam failure. On this occasion, massive amounts of debris were moved and deposited between stations 2 and 6, and a significant portion of the floodwater was stored in the wetland between stations 6 and 8 (Hillman 1998). The accumulated debris, which contained a considerable amount of wreckage from current and old beaver dams, was likely a rich source of DOC. It is possible that removal of the dams exposed buried deposits of organic matter to the stream water (Bilby and Likens 1980). We estimated that the failed dam released 7500 m^3 of water and that the flood peak took 20 min to travel down the 1660-m reach between stations 2 and 6.

Table 1. Stream-water dissolved organic carbon (DOC) concentrations for 10 locations on Rocky Creek in 1994–1995.

Station No.	Distance from station 1 (m)	*n*	Mean DOC concn. (mg·L^{-1})*
1	0	118	76.9 (2.04)a
2	1123	169	49.3 (0.35)b
3	1347	195	46.3 (0.47)c
4	1946	159	38.4 (0.59)d
5	2440	194	38.3 (0.68)d
6	2844	126	37.0 (0.71)d
7	3694	122	31.4 (0.41)e
8	5464	107	25.2 (0.32)f
9	6587	213	24.3 (0.40)f
10	6624	209	23.3 (0.31)f

*Values in parentheses show the standard error. Means with the same letter are not significantly different (Bonferroni (Dunn) *t* test).

The peak discharge of the flood wave was estimated to be 15–43 m^3·s^{-1} (Hillman 1998). An estimate of the peak DOC-carrying capacity of the flood wave was obtained by multiplying 15 m^3·s^{-1} (the minimum estimated peak discharge) by the mean DOC concentration along the path of the flood wave (A–B in Fig. 1) measured on 15 June 1994. The result (0.820 kg·s^{-1}) was an order of magnitude greater than the peak (0.040 kg·s^{-1}) of the greatest daily DOC-export event recorded during 1994–1995 (3426 kg·day^{-1} on 15 June 1994).

The occurrence of the second peak (3426 kg·day^{-1}) 1 week after the flood may be attributed to the 38 mm of rain that fell between 9 and 14 June. The increased flow resulting from the rainfall probably eroded the debris brought down by the flood, and also flushed downstream the DOC that had accumulated, along with the flood waters, in the wetland of area IV. Similarly, the third DOC peak (2676 kg·day^{-1}) on 4 July 1994 resulted from the 63 mm of rain that fell in the preceding 5 days (Fig. 2*b*), causing stream water levels to rise. This allowed the stream to erode channel debris left over from the flood that, previously, was above the water line. A fourth DOC peak (645 kg·day^{-1}), following 20 mm of rain, was recorded on 12 July 1994 (Fig. 2*b*). Evidently, the rain created a response in both the upper (Fig. 2*a*) and the lower (Fig. 2*b*) catchments because most stations showed a recession in DOC loads between 16 July and 1 August.

Antecedent soil water conditions also played a role in generating the high levels of DOC recorded in Rocky Creek between 9 June and 12 July 1994. The melting snow, which produced 35 mm of runoff during April, probably initiated soil-water recharge during ground thaw. The 179 mm of rain that fell between 5 June and 12 July 1994 also contributed to soil-water recharge and likely was instrumental in flushing DOC from the soil into the stream.

The runoff/rainfall relationships for the two main DOC-export events in June 1994 illustrate the interdependence of the two events and demonstrate the capacity of the wetland in area IV for retention storage (Fig. 3). The cumulative precipitation of 36.4 mm for 2–9 June resulted in 7.4 mm of

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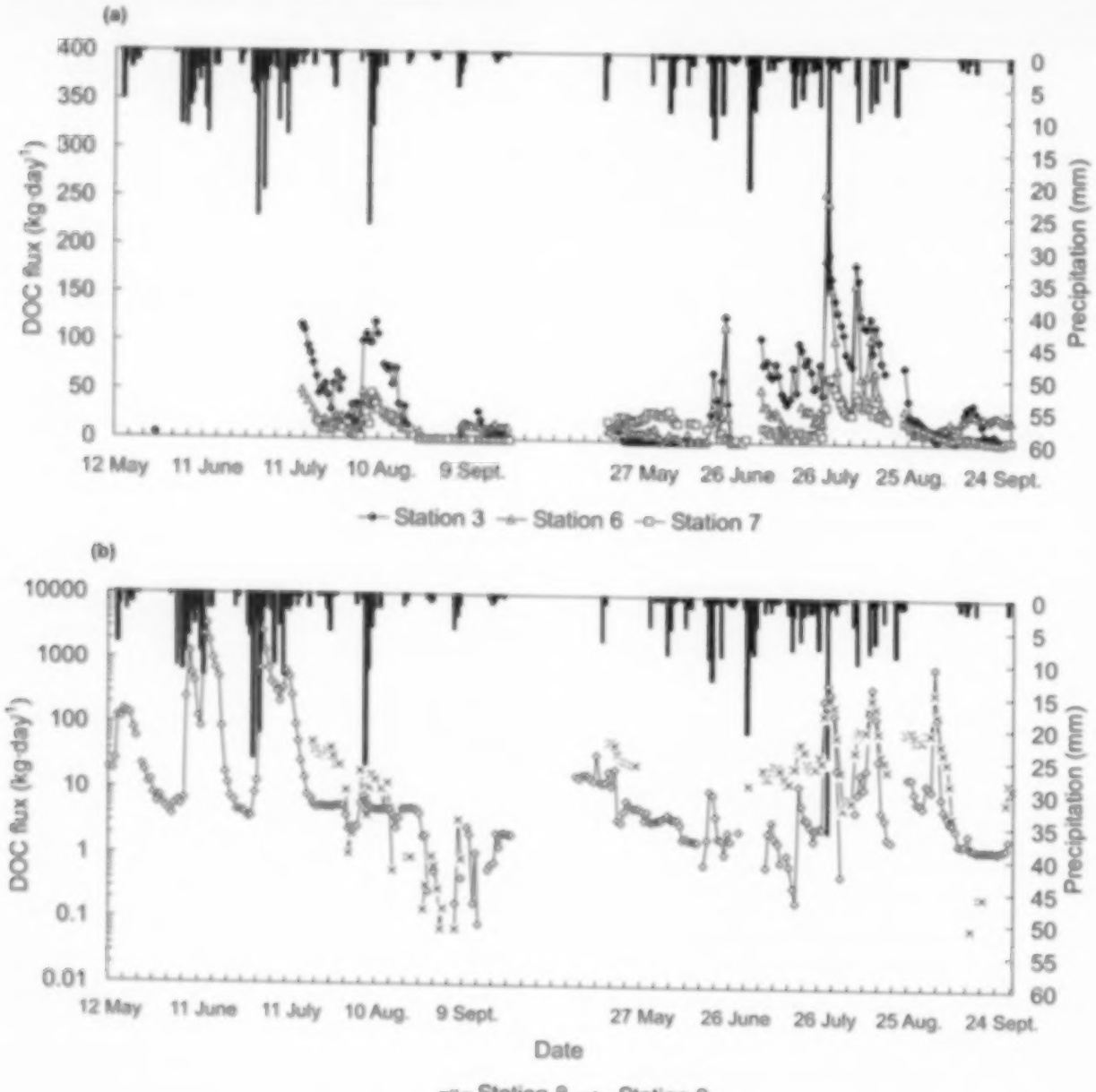
Fig. 2. Precipitation and dissolved organic carbon (DOC) fluxes from the upper catchment areas (*a*) and lower catchment areas (*b*) of Rocky Creek between May 1994 and September 1995.



runoff from the catchment, or 114 653 m^3 of water — 15 times the 7500 m^3 released by the failed dam. Thus, although the peak flow resulting from the beaver-dam failure was extreme above the wetland, the volume released, in terms of catchment outflow, was not. It is clear that the 7500-m^3 inflow of water, distributed over the 0.90-km^2 wetland, would increase the depth of water there by only 8.3 mm — an amount easily absorbed by the wetland.

Illustrating the importance of antecedent conditions, the runoff/precipitation ratio for June 2–9 was 0.20 (36 mm of precipitation) compared with 0.58 for June 10–14 (41 mm of precipitation). In the earlier period, basic storage capacity was available, but this became exhausted, so that in the later period a much larger proportion of the precipitation appeared as runoff (Hillman 1998).

On 8–9 August 1994, 38 mm of rain fell, producing a noticeable increase in DOC flux on the upper catchment (Fig. 2*a*). On the lower catchment, there was a slight increase in DOC flux at station 8 and a negligible response at station 9 (Fig. 2*b*). Therefore, DOC was either being stored

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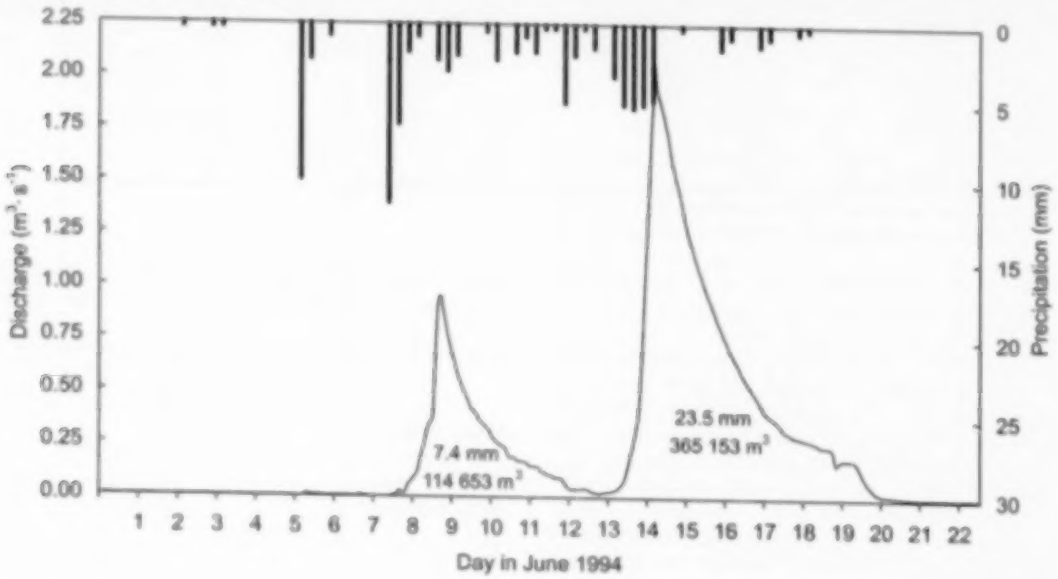
Fig. 3. Precipitation and hydrographs for station 9 (07GF006) in Rocky Creek at the time of the dam failure and immediately following that event. The numbers below the hydrographs indicate the depth of runoff and the volume of water released during each event (modified from Fig. 9 in Hillman 1998).



in the channel or being retained through other processes active in the channel.

The highest DOC fluxes among stations in 1995 were also recorded at station 9, on 30 July, 14 August, and 4 September, when the fluxes were respectively 476, 417, and 851 kg·day^{-1} (Fig. 2*b*). These values represent exports of DOC from Rocky Creek equal to 31, 27, and 55 kg·km^{-2}·day^{-1}. The first peak is certainly related to the 36-mm rainstorm that occurred on 30 July because DOC loads increased at all five measuring stations simultaneously, with the peaks increasing progressively downstream (Fig. 2).

Unlike the first 1995 peak, where DOC fluxes at the different stations peaked on the same day, maximum DOC fluxes at the different stations for the second peak were not concurrent (Fig. 2). These data suggest that the 14 mm of rain that fell on 8–9 August flushed DOC from the upper catchment (stations 3, 6, and 7) into the central wetland. The flushing action beyond the wetland (stations 8 and 9) was weak because the increase in DOC loading downstream from the wetlands was less substantial than the increase in DOC loading upstream. It took the additional 16 mm of rain that fell on 13–15 August to induce significant flushing of the wetland, thus significantly raising the levels of DOC in flow passing stations 8 and 9.

A different situation prevailed on 4 September, when the third DOC-loading peak occurred. In the upper catchment, DOC levels at stations 3, 6, and 7 were in recession, which was consistent with the fact that no rain had fallen in 10 days (Fig. 2*a*). In the lower catchment, however, DOC loads increased from 85 to 356 kg·day^{-1} at station 8 and from 11 to 851 kg·day^{-1} at station 9 (Fig. 2*b*). Evidently, the central wetland was the source of additional DOC and the sudden flushing probably resulted from a beaver-dam failure there. The large difference between the peak DOC fluxes recorded at stations 8 and 9 suggests that the difference in DOC and water volume may have been due to the amounts flushed from beaver ponds in the reach between the two stations.

Between episodic events, stream discharge and disturbances are minimal, and biological processes such as inorganic carbon assimilation, aerobic decomposition, and anaerobic decomposition govern the fate of stream DOC. The first reaction entails assimilation of inorganic carbon and its conversion to organic carbon, usually by algae. The second, a dominant reaction in aerated stream waters, involves the conversion of DOC to carbon dioxide and water. In beaver ponds and behind debris dams where sediments and organic matter accumulate, oxygen may become depleted and anaerobic decomposition may occur, producing methane and carbon dioxide (Thurman 1985).

Export of DOC from Rocky Creek

A summary of hydrological indices for the 3 years of record shows that although total precipitation in 1994 and 1995 was almost identical, water yield from the Rocky Creek catchment in 1994 was 3.7 times that in 1995 (Table 2). It is likely that wetter antecedent soil-water conditions and greater release of water from catchment storage were the principal factors governing the higher water yield in 1994. Peak flows from the catchment occurred in June of 1993 and 1994 and September of 1995.

The four major DOC export events, which occurred during a total of 28 days in 1994, accounted for 94% of the total DOC exported from Rocky Creek during the 1994 recording period. On a catchment basis, this is equivalent to an export of 1374 kg·km^{-2}. It is suspected, however, that most of the DOC transported during this period originated from debris in the channel of area III. Similarly, the three

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Table 2. Hydrologic indices for the Rocky Creek catchment.

	1993	1994	1995
Period of record*	1 June – 30 Sept. (122)	18 Mar. – 31 Oct. (228)	22 Mar. – 31 Oct. (224)
Precipitation (mm)	206	324	325
Mean discharge ($m^3 \cdot s^{-1}$)†	0.014 (0.001)	0.083 (0.002)	0.023 (0.001)
Peak flow ($m^3 \cdot s^{-1}$)	0.203 (27 June)	2.070 (14 June)	0.52 (4 Sept.)
Water yield (m^3)	147.6×10^3	1635.0×10^3	445.1×10^3
Runoff (mm)	9.5	105	29
Runoff/precipitation ratio	0.05	0.33	0.09

*Numbers in parentheses show the number of days.
†Numbers in parentheses show the standard error.

main events that occurred during a total of 17 days in 1995 accounted for 84% of the total DOC exported from Rocky Creek during the 1995 measuring period.

Total DOC exports from the Rocky Creek catchment for the period May to September in 1994 and 1995 were compared with exports from the adjacent 19.70-km^2 Bridlebit Creek catchment. The latter is similar to Rocky Creek but remains relatively undisturbed by humans, and organic soil on the catchment tends to be concentrated along the stream channels. Stream discharge and DOC concentrations were measured on the catchment for the same period as for Rocky Creek. Discharge data for 1967–1987 and the average DOC concentrations for 1994–1995 were used to obtain estimates of DOC exports from both catchments in other years. In all cases, DOC export from Bridlebit Creek was 1.5–3 times higher than export from Rocky Creek (Table 3).

Table 3. Water yields, mean dissolved organic carbon (DOC) concentrations, and DOC exports for Rocky Creek and Bridlebit Creek.

	Water yield (m^3)	DOC concn. ($mg \cdot L^{-1}$)*	DOC export ($kg \cdot km^{-2}$)
Rocky Creek			
1975 (dry year)	349 000	23.6 (0.29*)	531
1979 (wet year)	2 031 000	23.6 (0.29)	3090
1967–1987 (avg.)	933 737	23.6 (0.29)	1421
1994†	856 604	27.4 (0.30)	1513
1995†	192 339	19.9 (0.20)	247
Bridlebit Creek			
1975 (dry year)	748 000	36.6 (0.27)	1389
1979 (wet year)	2 677 000	36.6 (0.27)	4973
1967–1987 (avg.)	1 843 857	36.6 (0.27)	3426
1994†	1 243 405	37.4 (0.34)	2360
1995†	213 398	35.1 (0.34)	380

*Numbers in parentheses show the standard error.
†For the period May–September only.

Subcatchments: DOC storage and yields

Areas I and II form the uppermost region of the Rocky Creek catchment (Fig. 1) and, consequently, supply DOC and other water-borne constituents to downstream areas. The lake at the top of the catchment was not an integral part of the study, but a few water samples were taken on 2 August 1994 from the surface of the lake, near the shore and close to the fen. They yielded an average DOC concentration of 39.0 $mg \cdot L^{-1}$, which is within the range (20–50 $mg \cdot L^{-1}$) of DOC concentration usually associated with dystrophic lakes (Thurman 1985). The hydrodynamic relationships between the fen and the lake are unknown, but the lake's close proximity to the fen suggests that the lake may serve as a water-recharge area for the fen and that the fen, in turn, may supply DOC to the lake when flow conditions are suitable.

Results from this study indicate that the 2-km^2 fen is the primary source of DOC for area I and for the catchment as a whole. The DOC in the fen may be regarded as an autochthonous input at source, but as an allochthonous input once it enters the stream channel and beaver ponds. Deciduous species such as poplars (*Populus* spp.) and willows (*Salix* spp.) supply allochthonous DOC inputs into the stream in all areas of the catchment. The total DOC load contributed by area I, on days when data were available from all five stations, was 3–4 times that contributed by area II (Table 4). Peak DOC loads from area I were 2.5–3.0 times greater than peak loads from area II. During dry spells, no-flow conditions prevailed at stations 3 and 7 (Table 4).

The reach between stations 4 and 6 lies within a steep-sided valley and contains the steepest channel gradient (3%) in the catchment. Before the flood in June 1994, the reach appeared to offer little in the way of storage capacity for water and DOC. There were no obstructions or beaver ponds present and much of the time the water that trickled through stones on the streambed was turbulent and well mixed. During the flood, however, this reach sustained the most damage and received most of the debris, much of it sediment and remnants of old beaver dams. The channel was completely or partially blocked at two or three locations by a wall of trees and debris that had been knocked down or swept away by the flood wave. Along the riparian areas, root mats of willow and other riparian species were forcibly overturned. Within the reach there was significant sediment deposition: at one location a section of the channel was completely filled with sediment. Near station 6, where the channel becomes less steep as it enters the wetland, there was significant deposition of sediment and vegetative debris on the ground surface among the trees. It is likely that after the flood and especially during significant rainfall events this debris served as an important source of DOC.

Export of DOC from the catchment is controlled to a large degree by the wetland in area IV and by storage in the channel sections draining areas III and V (Fig. 4). During the period 21 July – 24 September 1994 the maximum export of DOC never exceeded 8 $kg \cdot day^{-1}$, whereas inputs of DOC from areas I and II reached 121 and 48 $kg \cdot day^{-1}$, respectively, in response to 43 mm of rain that fell on 8–10 Au-

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Table 4. Fluxes of dissolved organic carbon (DOC) passing the five hydrometric stations on Rocky Creek during the periods* 21 July – 24 September 1994 and 20 May – 26 September 1995.

	Station 3 (5.31 km^2; contributing area I)†		Station 7 (4.11 km^2; contributing area II)		Station 6 (6.42 km^2; contributing areas I and III)		Station 8 (14.59 km^2; contributing areas I, II, III, and IV)		Station 9 (15.51 km^2; contributing areas I, II, III, IV, and V)	
	1994	1995	1994	1995	1994	1995	1994	1995	1994	1995
Total DOC (kg)	1903	4397	503	1445	873	3106	479	4387	165	3384
Avg. DOC (kg·day^{-1})‡	40.5 (4.9)	57.8 (5.7)	10.7 (1.6)	19.0 (1.7)	18.6 (1.5)	40.9 (5.2)	10.2 (2.0)	57.7 (9.3)	3.5 (0.3)	44.5 (15.0)
Max. DOC (kg·day^{-1})	120.6	195.4	47.9	67.5	48.5	258.4	54.3	355.8	7.7	851.2
Min. DOC (kg·day^{-1})	2.7	0.0	0.0	1.7	5.7	8.8	0.0	0.0	0.0	0.0
n (days)	47	76	47	76	47	76	47	76	47	76
DOC export (kg·km^{-2})	358	828	122	352	136	484	33	301	11	218

*These periods comprise days when data were available from all five stations simultaneously.
†Catchment area upstream from the station.
‡Numbers in parentheses show the standard error.

gust. Most of this input was stored in the wetland and in the channel of area III (Fig. 4*a*).

Similarly, between 16 May and 26 July 1995 the maximum DOC export recorded was 13 kg·day^{-1} and inputs during that time were stored primarily in the channel of area III (Fig. 4*b*). The period 27 July – 30 September 1995 was marked by three significant DOC export events. The first was in response to the 36 mm of rain that fell on 30 July, when the maximum DOC export reached 476 kg·day^{-1} (Fig. 4*c*). The storm was of a magnitude sufficient to flush significant quantities of DOC from storage, primarily from the wetland in area IV. A similar response, this time to two rainstorms, occurred on 14 August, when DOC export peaked at 417 kg·day^{-1}.

In 1995, the greatest amount of DOC (851 kg·day^{-1}) was exported from Rocky Creek on 4 September (Fig 4*c*). Areas IV and V contributed 97% of this amount. The minimal input of DOC from the upper catchment, together with the sudden flush of DOC from areas IV and V, suggests that a beaver-dam failure in area IV produced a flood wave that may have resulted in a second beaver-dam failure in area V.

DOC concentration

There was a marked, progressive decline in mean DOC concentrations from the top of the catchment to the outlet at station 10 (Table 1), the high DOC concentrations obtained immediately below the fen suggesting that the fen is a major source of DOC. The high stream DOC concentrations recorded in Rocky Creek generally are attributed not only to the presence of the fen but also to the catchment's generally flat and gently rolling topography, which allows water to remain in the catchment a relatively long time, facilitating prolonged leaching of litter and soil organic carbon.

The progressive decrease in DOC concentrations downstream may have been the result of either dilution or the uptake of DOC by biotic and abiotic factors. The addition to the stream of soil-water seepage and groundwater flow that are poor in DOC is one obvious dilution mechanism, but soil-water seepage and groundwater on the Rocky Creek catchment are rich in DOC (Fig. 5) and would probably contribute to higher stream DOC concentrations. At stations 3 and 9, DOC concentrations in water from all slope positions were 56–71% lower than corresponding stream concentrations, while at the midslope near station 4 and the bottom of the slope near station 5, DOC concentrations were 13% and 14% higher, respectively, than DOC concentrations in the stream. It is more likely that a number of mechanisms, particularly those related to DOC uptake and retention, are operating on DOC in such a way that the net effect is a progressive decline in concentrations downstream.

DOC concentrations in Rocky Creek showed distinct patterns over time depending on the season in which they were measured and the location along the stream. Fluctuations at stations 2, 3, 6, 8, and 9 were similar in that they fluctuated in response to rainstorms and tended to decrease with time in 1994 (Fig. 6*a*). In 1995, DOC concentrations at these stations increased from a low in the spring, peaked in late July, and decreased steadily in the fall. No significant fluctuations in DOC concentration occurred in 1995 despite rainfalls of 23 and 36 mm.

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Fig. 4. Precipitation and change in dissolved organic carbon (DOC) storage for the five subcatchments of Rocky Creek in 1994 (*a*), and 1995 (*b* and *c*). On 4 September 1995, 851 kg of DOC were exported from Rocky Creek.

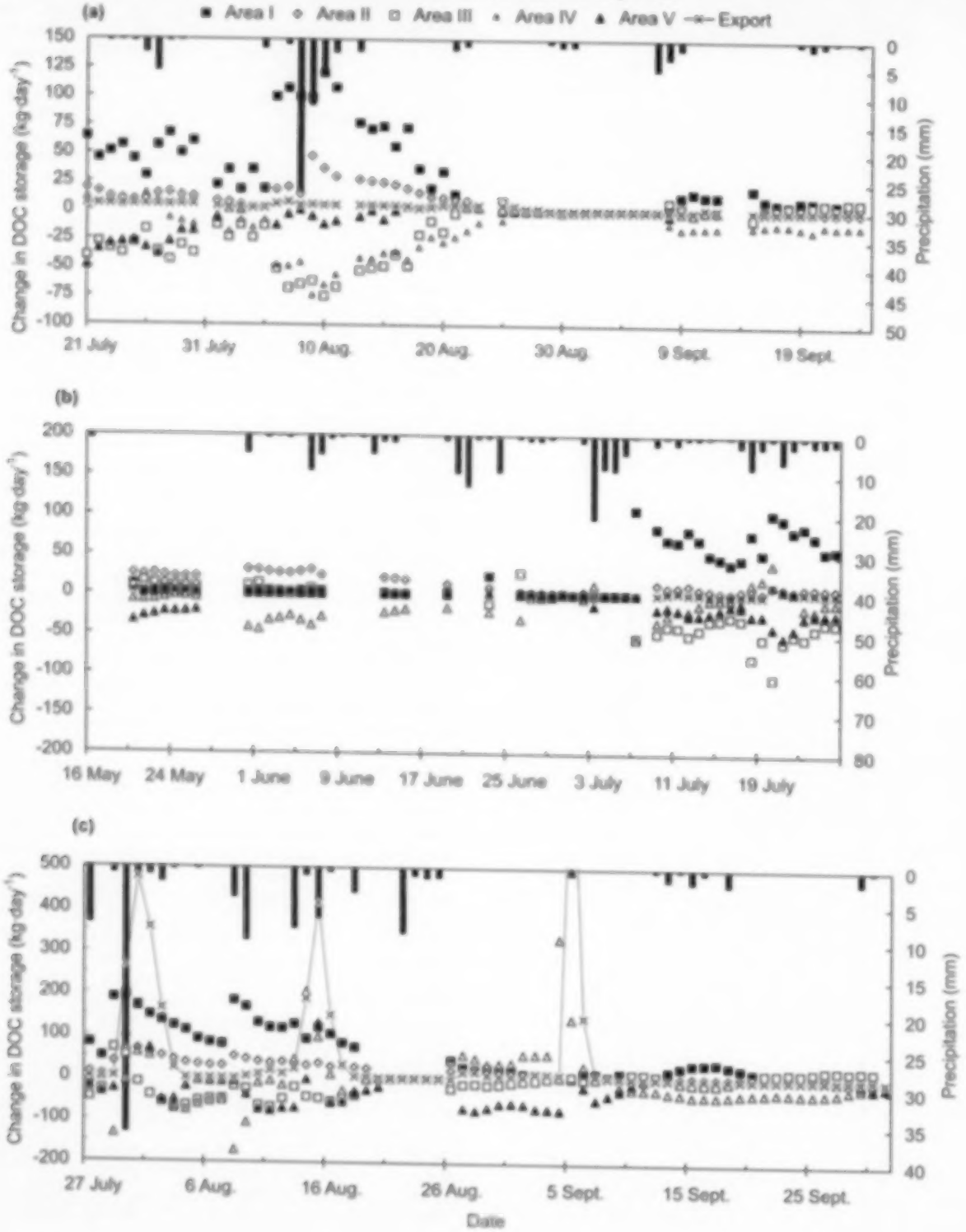

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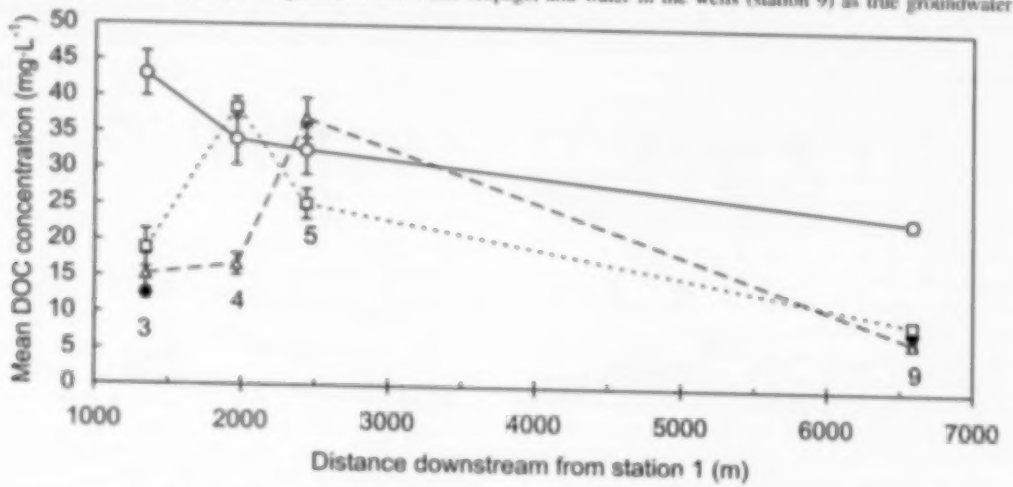
Fig. 5. Means and standard error bars for dissolved organic carbon concentration (DOC) in the stream (○) and in water taken from locations at the top (★), middle (□), and bottom of the slope (△) near stations 3, 4, 5, and 9 in 1993–1995 (n = 3–14. No samples were obtained from the piezometers at the top of the slope above stations 4 and 5 because these piezometers were always dry. Water in the piezometers (stations 3, 4, and 5) may be regarded as soil-water seepage, and water in the wells (station 9) as true groundwater flow.



DOC concentration at station 1 did not follow these trends. Instead, it increased steadily from a low recorded at the time at which measurement commenced to a high recorded when sampling for the year was discontinued (Fig. 6*a*). This steady increase suggests that enrichment was taking place and we speculate that the beaver pond located immediately downstream was the source of the enrichment. In 1994 and 1995, the area around station 1 was flooded by backwater from the beaver pond. Thus, in 1994 the stage at station 1 increased 23 cm, from a minimum in late June to a maximum in mid-August, after which the stage fell steadily to a minimum in early October, when measurement ceased. The pattern was repeated in 1995, only this time the stage increased 26 cm and peaked in early July. The propensity for natural obstructions in streams, such as organic-debris dams and beaver dams, to retain organic carbon is well documented (Bilby 1981; Naiman et al.1986; Smith et al. 1991). Given the foregoing situation, it is reasonable to assume that although the main supply of DOC originated in the fen, additional DOC may have been supplied through flooding by DOC-enriched backwater.

Fluctuations in DOC concentration at station 7 showed similarities common to those at stations 1 and 6. In 1994, DOC concentrations fluctuated in response to rainfall at stations 6 and 7, but in 1995, the DOC concentration at station 7 showed an increasing trend similar to that at station 1. The reason for this increasing trend at station 7 is not clear.

If the data for station 1 are excluded, the range of DOC concentrations reported here (15.2–62.4 mg·L^{-1}) is similar to concentration ranges reported for other studies conducted on different landscapes in Canada. Eckhardt and Moore (1990) found DOC concentrations ranging from 1.7 to 73.4 mg·L^{-1} in 42 Quebec streams and Gorham et al. (1998) measured DOC concentrations in the range 2.5–63.0 mg·L^{-1} in 42 Nova Scotia streams.

Correlations between the logarithm of mean daily discharge and DOC concentration at the catchment outlet were not significant ($p > 0.05$): less than 10% of the variation in DOC concentration was associated with discharge (Fig. 6*b*). Plotting DOC concentration against the logarithm of hourly discharge (hour at which DOC was sampled) did not improve the correlation. These results are consistent with those of Eckhardt and Moore (1990) and Hinton et al. (1997), who found poor correlations between discharge and DOC concentration on catchments containing wetlands, in contrast to high correlations where wetlands were absent. On the Rocky Creek catchment, more than 25% of the area is occupied by wetlands that developed naturally or were created by beaver. Gorham et al. (1998) reported a significant relationship between DOC concentration and the percentage of wetlands in 42 Nova Scotia streams.

In light of these results, we attempted to find a relationship between mean DOC concentration and wetland area on the Rocky Creek catchment, even though the subcatchments are nested rather than independent. We found the relationship to be significant (p = 0.034) and it accounted for 63% of the variation in DOC concentration (Fig. 6*c*). The DOC concentration at station 7 appears to be high for the relatively low amount of wetland that occurs upstream in area II. We speculate that some of the fen water originating in area I discharges into area II (Fig. 1), thereby enriching water flowing through area II and past station 7.

Disturbance–DOC relationships

It is clear from the preceding discussion that the transportation of large amounts of DOC down the catchment related directly to events that created major disturbances, such as high rainfall or the breaching of beaver dams. Both types of events produced large volumes of water moving at greater than normal velocities and considerable amounts of DOC. It is the flushing action of the high-volume, high-velocity water that releases DOC from its substrate. Outside of these events, exports of DOC from Rocky Creek rarely exceeded 10 kg·day^{-1}. It appears that there are two main sources of DOC in the Rocky Creek catchment: the areas from which runoff flows into the channel and the channel itself. The first

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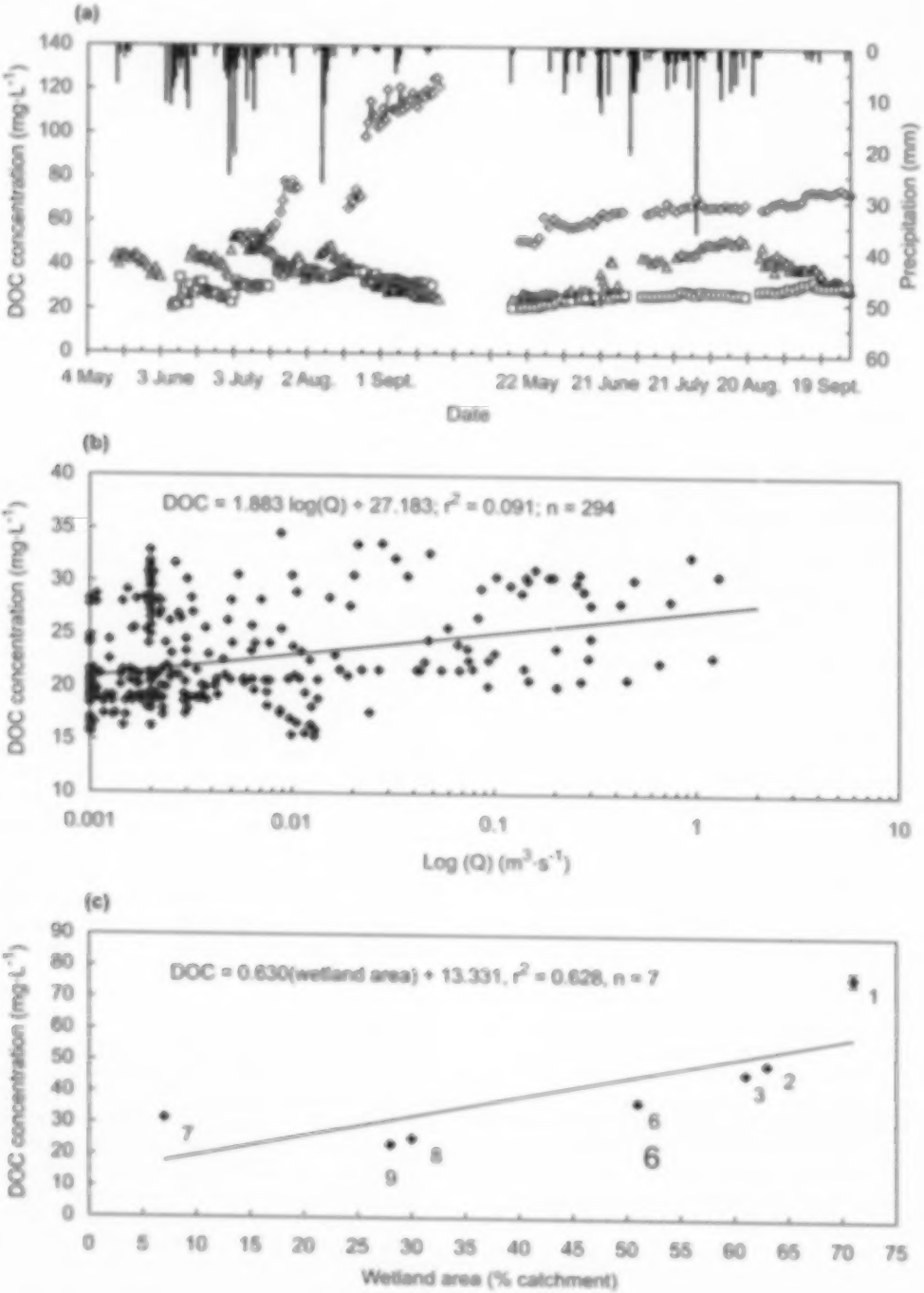
Fig. 6. (*a*) Fluctuations of dissolved organic carbon (DOC) concentration at three stations (1 (◇), 6 (△), and 7 (□)) during seasonal changes and significant episodic events on Rocky Creek in 1994 and 1995. Fluctuation patterns at stations 2, 3, 8, and 9 (not shown) were similar to that at station 6. A file containing data for these stations is available from the corresponding author. (*b*) Regression between the logarithm of mean daily discharge and DOC concentration at the outlet of the Rocky Creek catchment. (*c*) Regression between wetland area and DOC concentration (●) on the Rocky Creek catchment. The station number near each data point indicates that the wetland area was computed from the total catchment area that lies upstream from that particular station. The solid line indicates the predicted DOC concentration.



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is an area source and the second, characterized by organic-debris dams and beaver impoundments, more closely approximates a point source. Landscape features such as the fen and the central wetland may be considered specialized forms of an area source.

The catastrophic beaver-dam failure that occurred on 8 June 1994 may have released considerable DOC stored behind the beaver dam that failed originally and behind those dams subsequently ruptured by the flood wave. The debris torn out of the banks by the flood wave may also have served as an additional source of DOC. Before the beaver dam failed, the lower section of channel between stations 4 and 6 draining area III was completely free of debris and likely was not a location in which DOC was readily stored. During the passage of the flood wave, however, the channel was blocked at several locations with massive amounts of debris that effectively acted as organic-debris dams.

The organic-debris dams formed by the flood wave on Rocky Creek differ in two respects from most other organic dams in headwater streams. They consisted of very large (whole) trees as well as fine material, and were formed at an extremely high discharge rate, whereas debris dams in small streams usually consist of smaller material and are formed as a result of low flows (Bilby and Likens 1980). Organic-debris dams are very important components of small stream ecosystems because they retain the organic material that serves as an energy source for stream organisms. They allow the organic material to be processed into finer size fractions in headwater tributaries rather than transported downstream in course particulate form (Bilby and Likens 1980; Bilby 1981). Organic-debris dams are being increasingly recognized as an ecologically desirable attribute of headwater streams rather than obstruction material that should be removed (Dolloff and Webster 2000).

The data from this study indicate that channel obstructions may serve as both storage and source areas. The greatest increases in daily DOC concentrations were observed at station 6, which is the first hydrometric station downstream from the newly created obstructions. Although no other meaningful data were obtained at station 6 at the time of the flood, DOC concentrations at station 6 increased more than 50% during the 2 days after the 51-mm rainfall of 1–3 July 1994. Similarly, concentrations at the station increased 40% in response to the 38 mm of rain that fell on 7 and 8 August 1994. Sudden increases in DOC concentrations of this magnitude were not observed at the other stations. By implication, it would appear that a significant proportion of the DOC exported from Rocky Creek in June and early July 1994 originated from the material deposited in the channel of area III and among the trees near station 6. This would be in addition to the amount of DOC provided by the contributing area of area III.

The lake, wetlands, beaver impoundments, and organic-debris dams that characterize the Rocky Creek catchment play a critical role in the capture and release of water and DOC. Beaver impoundments are particularly important for organic-matter storage and processing (Naiman et al. 1986). They influence DOC export by increasing the water surface area in contact with organic sediments and increase particulate organic matter export by adding massive amounts of debris to the stream channel (Naiman 1982). Streams with considerable beaver activity export substantially more DOC than streams not affected by beaver (Naiman 1982), and DOC concentrations downstream from beaver dams are usually greater than the concentrations upstream from the dams (Smith et al. 1991).

In conclusion, natural disturbances such as high rainfall and beaver-dam failures can result in the movement of substantial quantities of DOC through a stream system. A 2.3-km section of Rocky Creek was drastically altered when the flood wave resulting from the breached beaver dam created several organic-debris dams by depositing large amounts of debris and sediment within the section. Although a substantial amount of DOC was exported (peak of 1274 $kg \cdot day^{-1}$) from the catchment at the time of the flood, considerably more was exported during subsequent events (peaks of 3426 and 2676 $kg \cdot day^{-1}$). Results from stream DOC storage analyses suggest that the organic-debris dams created by the dam-failure dam event served as both sources and sinks for DOC, and that DOC storage on the catchment was strongly influenced by the presence of wetlands and beaver. Organic-debris dams are being increasingly recognized as an ecologically desirable attribute of headwater streams. In 1994, disturbances that were active for a total of 17 days accounted for 94% (1374 $kg \cdot km^{-2}$) of the DOC exported from the catchment. In 1995, disturbances occurring during a total of 28 days accounted for 84% (204 $kg \cdot km^{-2}$) of exported DOC.

The highest mean DOC concentration in the stream (77.0 $mg \cdot L^{-1}$) was recorded near the top of the catchment, where a 2-km^2 fen served as the primary source of DOC. Concentrations of DOC decreased progressively downstream to the catchment outlet, where the DOC concentration averaged 23.3 $mg \cdot L^{-1}$. There was no significant correlation between the logarithm of mean daily discharge and DOC concentration at the catchment outlet but there was a significant correlation between DOC concentration at a point in the stream and the amount of wetland area in the catchment upstream from that point.

Beaver impoundments are such specialized features of the landscape that Johnston and colleagues (Johnston and Naiman 1987; Naiman et al. 1988) introduced the concept of "patch bodies" so that the effects of beaver activity could be integrated into contemporary river continuum models (e.g., Vannote et al. 1980). Patch bodies are defined as volumetric landscape units that have surficial boundaries with upper and lower strata, and lateral boundaries with adjacent patches within the same stratum. Patch bodies created by beaver impoundments include the beaver pond, the aerobic soil beneath the pond, and the underlying anaerobic soil (Johnston and Naiman 1987; Naiman et al. 1988). Because beaver have such a profound effect on the riverine and riparian environments it has been recommended that, where applicable, beaver should be integrated into resource-management planning as well as considered in the development of stream ecosystem theory (Naiman et al. 1986).

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The role of ultraviolet radiation in structuring epilithic algal communities in Rocky Mountain montane lakes: evidence from pigments and taxonomy

Suzanne E. Tank and David W. Schindler

Abstract: We investigated changes in the community structure of epilithic (rock-dwelling) algae brought about by ultraviolet-A and -B radiation (UV-A and UV-B, respectively), using measurements of biovolume of individual taxa, and taxonomically diagnostic photosynthetic pigments. We undertook our study in four Canadian Rocky Mountain montane lakes, where downwelling ultraviolet radiation (UVR) can be intense. Although taxonomic counts revealed significant decreases in algal community diversity under UV-A and UV-B exposure, they revealed no other significant trends in algal community composition. Instead, redundancy analysis using these counts suggested that variations in nutrient concentrations were most important in structuring these communities. Photosynthetic pigments decreased significantly under UV-A and UV-B exposure. This decrease was much more striking for carotenoid than for chlorophyll concentrations, despite the photoprotective properties of many carotenoid pigments. Grazed carotenoids have been shown to be more resistant to degradation than grazed chlorophylls. We suggest that an observed increase in grazing pressure in our UVR-shielded communities counteracted increases in algal growth, but that increased algal growth rates were reflected by increased concentrations of slowly degrading carotenoids. Our study suggests that other factors, such as nutrients and grazers, are more important than UVR for structuring epilithic algal communities in our study lakes.

Résumé : Nous avons étudié les changements dans la structure des communautés d'algues épilithiques (qui colonisent les pierres) causés par les radiations ultraviolettes A et B (UV-A et UV-B) en mesurant le biovolume des taxons individuels et les pigments photosynthétiques importants pour la détermination taxinomique. Nous avons entrepris notre travail dans quatre lac de montagne des Rocheuses canadiennes où la pénétration de la radiation ultraviolette (UVR) peut être intense. Bien que les dénombrements taxinomiques révèlent un déclin significatif de la diversité de la communauté d'algues à l'exposition à l'UV-A et l'UV-B, aucune autre tendance dans la composition de la communauté d'algues n'est apparente. Au contraire, une analyse de redondance faite sur ces dénombrements indique que les variations dans la concentration des nutriments sont plus importantes dans la structuration de ces communautés. Les concentrations de pigments photosynthétiques décroissent de façon significative à l'exposition à UV-A et UV-B. Ce déclin est beaucoup plus spectaculaire chez les concentrations de caroténoïdes que de chlorophylles, malgré les caractéristiques photoprotectrices de nombreux pigments caroténoïdes. Il est connu que les pigments caroténoïdes soumis au broutage sont plus résistants à la dégradation que les chlorophylles. Nous croyons que l'augmentation de la pression de broutage observée dans nos communautés protégées de la UVR contrebalance l'augmentation de la croissance des algues, mais que les taux accrus de croissance des algues se reflètent dans l'augmentation des concentrations de caroténoïdes en train de subir une lente dégradation. Notre étude indique que d'autres facteurs, tels que les nutriments et le broutage, sont plus importants que la UVR pour structurer les algues épilithiques dans les lacs que nous avons étudiés.

[Traduit par la Rédaction]

Introduction

The effect of ultraviolet radiation (UVR) on photosynthesizing organisms is not constant across either species or environments. Different taxa vary widely in their response to UVR exposure (Jokiel and York 1984), which may lead to changes in community structure (Worrest et al. 1981). Despite this, in situ studies of how UVR affects the community structure of benthic primary producers have been few.

The effect of UVR on algal community structure might be influenced by several factors. Alterations in light quality and the interplay between different wavelengths can fundamentally alter the UVR response of photosynthesizing organisms (Cullen and Neale 1994). Ultraviolet-A radiation (UV-A) has

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been shown to trigger both cellular repair mechanisms (Quesada et al. 1995) and the production of UVR-absorbing pigments in some algal species (e.g., Carreto et al. 1990). Variations in ambient temperature may also regulate the response to UVR. For example, the rate of repair of UVR-induced damage can decrease at lower temperatures (Roos and Vincent 1998). In addition, the nutrient status of the cell can influence UVR susceptibility. In some studies, extremely nutrient-limited algae have shown little response to fluctuations in UVR exposure (Behrenfield et al. 1994; Xenopoulos et al. 2002), suggesting that in severely nutrient-stressed environments nutrient availability, rather than UVR, may regulate growth and production.

Before the onset of changes in community structure, however, it is likely that algal species will undergo physiological changes as a result of UVR stress. Although they are often used to infer algal abundance (Millie et al. 1993), changes in pigment concentrations within algal cells have been well documented in high-UVR environments. UVR stress has been shown to bleach photosynthetic pigments (e.g., Döhler and Buchmann 1995). However, over the long term, several investigators have observed increasing carotenoid concentrations, or increases in carotenoids relative to chlorophylls (e.g., Paerl et al. 1983; Goes et al. 1994), which may confer photoprotective ability upon the cell. Changes in growth rates, nutrient availability, and grazing pressure may further affect pigment concentrations within algal communities (Chalup and Laws 1990; Poister et al. 1999).

In this study, we experimentally investigated changes in the community structure of epilithic (rock-dwelling) algae brought about by both UV-A and ultraviolet-B radiation (UV-B), through the analysis of taxonomic counts and photosynthetic pigments. This study was conducted simultaneously in four montane lakes of varying water transparency, to examine differences in response caused by previous and current UVR exposure. We further investigated whether our two methods of assessment were congruent; that is, whether the analysis of epilithic algal composition using taxonomic counts and pigment signatures provided equivalent results. Our analyses place UVR in the context of other environmental factors, such as nutrients, alkalinity, and temperature, and assess its relative role in structuring epilithic algal communities.

Methods

Study lakes

Our experiments were conducted in four oligotrophic lakes of Jasper National Park. Honeymoon, Leach, Hibernia, and Saturday Night lakes lie in the main ranges of the Canadian Rocky Mountains, and are underlain by calcareous till (Holland and Coen 1983). The lakes lie at similar elevations (1198–1418 m above sea level); however, because of microclimatological differences, Leach, Hibernia, and Saturday Night lakes are located in the montane ecoregion, while Honeymoon Lake lies in the lower subalpine region. The lakes were chosen to span a gradient of water clarity: Leach and Honeymoon lakes are relatively clear and have high UVR penetration (1% UV-B penetration in summer = 0.71–0.98 m), while Hibernia and Saturday Night lakes are much less transparent (1% UV-B penetration in summer = 0.34–0.46 m).

Experimental design

We used three optical screening treatments (Cadillac Plastics, Edmonton, Alberta) to test the effects of UVR on epilithic communities. The first, our "photosynthetically active radiation (PAR) + UV-A + UV-B" treatment, allowed penetration of the full solar spectrum (Acrylite OP4®, 70% cutoff at 280 nm). The second, our "PAR + UV-A" treatment, blocked UV-B radiation (Mylar-D®, 70% cutoff at 320 nm). The third, our "PAR" treatment, blocked all UVR (Acrylite OP3®, 100% cutoff at 400 nm). The Plexiglas® and Mylar sheets were suspended slightly below the water surface using a frame of ABS piping. Artificial substrata (acid-washed unglazed ceramic tiles, 23 cm^2) were placed on the lake bottom below the plastic screens. The positioning of the screening treatments relative to the tiles ensured constant filtration of incoming radiation despite daily and seasonal solar-angle shifts. The tiles were initially placed at a depth of 30 cm and were monitored throughout the summer for changes in depth.

One replicate of each of the three UVR-screening treatments was set up in each of the four study lakes. Experiments were set up between 26 and 31 May 2000 and samples collected on days 40, 60, and 80 thereafter. Samples were collected by randomly selecting tiles, and scraping off the epilithic community that had accumulated on the tile surface. For photosynthetic pigments, four replicate samples consisting of one tile each were filtered on Whatman® GF/F filters and frozen. For algal taxonomy, four replicate tile samples were combined to form a single sample, and immediately preserved using Lugol's solution. On each sampling occasion, a water sample was collected from immediately below the surface at the deepest point of the lake and analysed for general water chemistry using standard methods (Stainton et al. 1977; Prepas and Rigler 1982; American Public Health Association 1992). To account for differences in invertebrate abundance when considering algal taxonomic shifts, samples of invertebrates were collected from three replicate tiles and preserved in 4% formalin until the time of counting.

Determination of water clarity

Every 10 days after experimental setup, water was collected from the center of the lake immediately below the surface. Water samples were kept in the dark and refrigerated until analysis (within 2 weeks), at which time light absorption in the range 280–700 nm was measured through a 2-cm cuvette using a scanning spectrophotometer (Cary 50 UV-Vis spectrophotometer, Varian Inc., Palo Alto, California).

Laboratory analyses

Epilithic pigments

Epilithic-pigment composition was determined using reverse-phase high performance liquid chromatography (HPLC; Leavitt and Carpenter 1990). Two replicate filters containing epilithon were combined and freeze-dried overnight (Hansson 1988), directly immersed in 10 mL of extraction solvent (85% acetone, 15% methanol by volume), sonicated, and allowed to extract in the dark for 24 h at

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4 °C. Extracted samples were filtered through 0.2 µm membrane filters, evaporated to dryness, and frozen under nitrogen gas until the time of analysis. Dried extracts were dissolved in a known volume of injection solvent (70% acetone, 25% ion-pairing reagent, 5% methanol by volume) containing 3.2 mg·L^{-1} of the internal standard Sudan II. Pigments were separated on a Hewlett Packard Model 1100 HPLC equipped with inline diode array detector and fluorescence detector and a 10-cm Varian Microsorb C18 column with 100-Å (1 Å = 0.1 nm) beads.

Algal taxonomic composition

Preserved algal samples were sonicated for two 15-s intervals at 20 kHz (Sonifier Cell Disruptor, Model W140, Heat Systems – Ultrasonic Inc., Plainview, New York), and a 2-mL aliquot was removed, stained with Fast Green FCF (Fisher Scientific), and allowed to settle overnight. Algal cells were identified to lowest taxonomic unit. Cells in random fields were enumerated until 100 viable cells of the dominant taxon had been observed, at which time the final field was completely counted. Viable cells were distinguished by the presence of cellular structures stained with Fast Green FCF (Owen et al. 1978). Approximations of cell volumes of each species were made according to best-fit formulae for different taxa, and converted to wet-biomass estimates (Nauwerck 1963).

Statistical analyses

Richness and diversity

Algal community richness was calculated as the total number of species present in each sample under each screening treatment. Shannon–Wiener and Simpson's diversity indices were calculated using common formulae; calculation of the Shannon–Wiener index was performed using logarithms to the base of 2, while Simpson's index is represented as D. Two-way analyses of variance (ANOVAs) were used to test for the effects of UVR treatment on algal richness and diversity indices (JMP® version 3.2, SAS Institute Inc. 1997). Data were analysed as the difference between a given UVR treatment and the PAR-only treatment, to account for differences in richness and diversity values among lakes. The Tukey–Kramer test was used for post-hoc comparisons where analyses were significant (SYSTAT® version 8.0, SPSS Inc. 1998).

Direct gradient analysis

The relationship between algal community composition and environmental factors was investigated using ordination analysis (CANOCO version 4; ter Braak and Šmilauer 1998). Detrended correspondence analysis was first performed to determine whether linear (e.g., redundancy analysis, RDA) or unimodal models (e.g., canonical correspondence analysis) best suited the data set (ter Braak and Šmilauer 1998).

Values for algal biomass and environmental variables were log-transformed to downweight the importance of large-celled taxa, which might otherwise dominate the analysis (ter Braak and Šmilauer 1998), and to approximate normality. Throughout our analyses, Monte-Carlo permutations were restricted by specifying repeated samples from one experimental replicate as members of a time series (ter Braak and Šmilauer 1998). The environmental data set was screened for redundant variables to eliminate those variables that did not exert a significant influence on algal distributions. A preliminary RDA was run with forward selection to rank the variables in order of percent taxonomic variance explained by each. The RDA was inspected for environmental variables with high variance-inflation factors (VIF), outlier variables, and variables that did not significantly improve the fit of the model. Variables with high VIF were removed from least significant variable to most, until all inflation factors were less than 20 (ter Braak and Šmilauer 1998). Nonsignificant variables, and those that skewed the model fit, were further removed. The significance of the final RDA model was determined by testing the eigenvalues of each of the first four canonical axes (Monte-Carlo test with 199 permutations).

In RDA, the lengths of the arrows representing environmental variables correspond to their importance in explaining the observed variance in the species data. The proximity of the arrows to one another represents their similarity: environmental variables whose arrows are close together are highly positively correlated, while those with arrows at a 90° angle to one another are not related, and those with arrows facing in opposite directions are highly inversely related. Likewise, species points placed close together in the ordination diagram are more similar than points far apart, and two species points found in close proximity to one another will be found under similar conditions. The relationship between a species and a given environmental variable is obtained by projecting a line from the species point to the arrow representing the environmental variable, at an angle perpendicular to the environmental variable. The farther along the arrow in the positive direction this projected line falls, the more positively correlated with the environmental variable is the species (ter Braak 1994).

Analysis of pigment composition

The effects of UVR on log-transformed concentrations of chlorophyll and carotenoid pigments, and chlorophyll *a* to carotenoid ratios, were analysed with two-way multivariate analysis of variance (MANOVA) (JMP® version 3.2, SAS Institute Inc. 1997). Further investigation of individual chlorophyll and carotenoid concentrations and pigment ratios under the UVR-screening treatments was done using two-way ANOVAs. When a significant result was present in the MANOVA analysis, Dunn–Šidák-adjusted contrasts were performed (JMP® version 3.2, SAS Institute Inc. 1997). Significant differences in two-way ANOVA results were investigated using the Tukey–Kramer test (SYSTAT® version 8.0, SPSS Inc. 1998).

Results

Incident radiation and water clarity and chemistry

A detailed description of total downwelling UV-B, UV-A, and PAR during the experimental period is given in Tank et al. (2003). Spectrophotometric estimates of water clarity showed that Hibernia and Saturday Night lakes absorbed strongly in the UV-B range, while Leach and Honeymoon lakes were more transparent (Fig. 1). In the more coloured lakes, less than 10% of incident UV-B reached the tile surface during the experimental period. The difference in trans-

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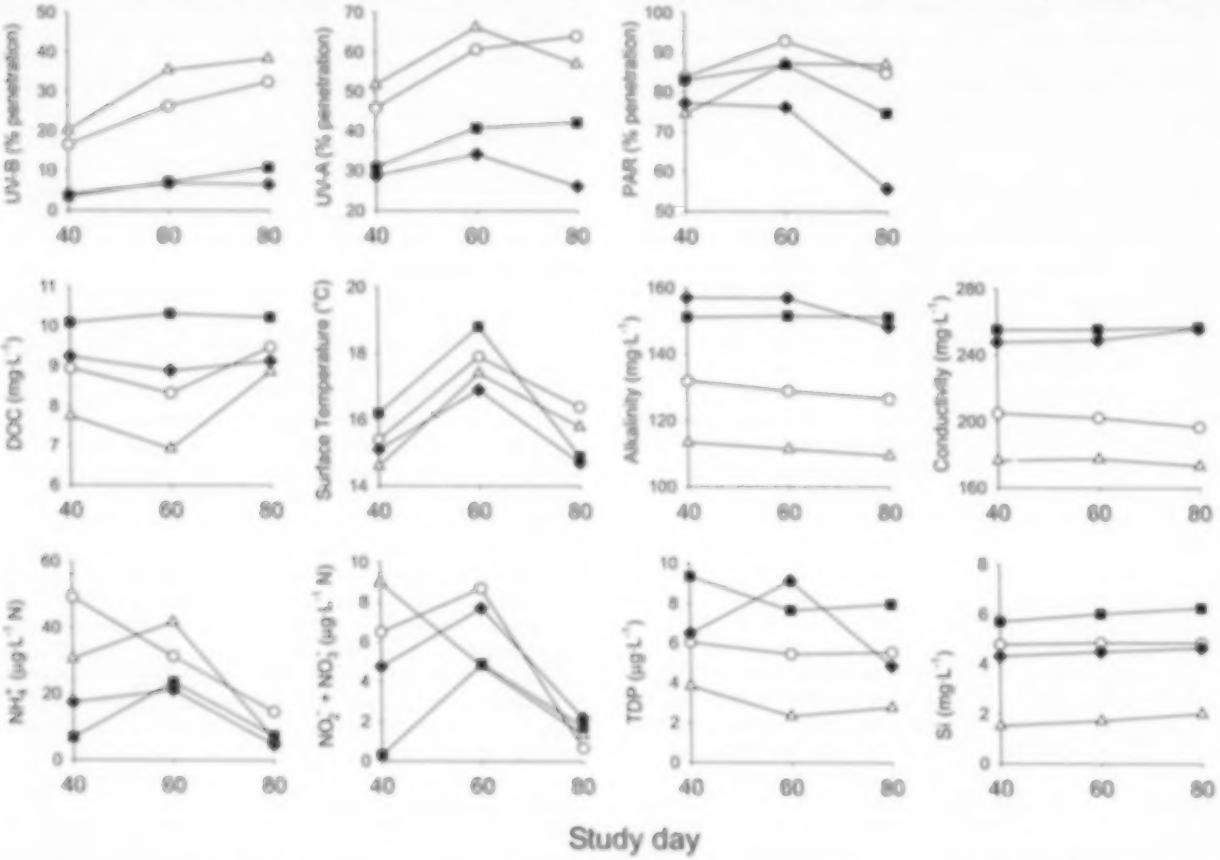
Fig. 1. Limnological parameters for four study lakes in Jasper National Park, Alberta, Canada (○, Leach Lake; △, Honeymoon Lake; ■, Hibernia Lake; ◆, Saturday Night Lake). Measurements were taken every 20 days from early June to late August 2000. Alkalinity is measured as HCO_3^-. UV-B, ultraviolet-B radiation; UV-A, ultraviolet-A radiation; PAR, photosynthetically active radiation; DOC, dissolved organic carbon. PAR, UV-A, and UV-B were measured as percent penetration of downwelling radiation to the experimental depth.



parency between the lakes decreases with increasing wavelength, to the point where absorption is almost identical in the PAR region, with the exception of Saturday Night Lake (Fig. 1).

The two transparent lakes, Leach and Honeymoon, had lower concentrations of total dissolved phosphorus (TDP), alkalinity, and conductivity, and higher concentrations of NH_4^+ (Fig. 1). Concentrations of Si were lowest in Honeymoon Lake and similar in the other three lakes. Dissolved organic carbon (DOC) concentrations were higher than expected in Leach and Honeymoon lakes, given their clarity, suggesting high concentrations of autochthonous carbon in these lakes (Tank et al. 2003). NO_2^- + NO_3^- concentrations showed no clear trends between lakes. Although nitrogen concentrations decreased as the summer progressed, this trend does not appear in the phosphorus data (Fig. 1).

Algal taxonomy: species richness and diversity

Epilithic species richness varied between 12 and 26 species in all treatments for all dates, and did not show a trend with time (Fig. 2; $F_{[2,27(\text{time})]} = 0.36$, $p = 0.703$). A combined analysis for all four of the study lakes showed no significant UVR effect (Fig. 2; $F_{[2,27(\text{UVR})]} = 1.49$, $p = 0.243$; $F_{[4,27(\text{interaction})]} = 0.12$, $p = 0.975$). Although visual inspection of the data suggests that UVR may significantly decrease richness in the two clear study lakes (Leach and Honeymoon), an analysis of these two lakes alone was also not significant ($p_{\text{UVR}} = 0.0958$, $p_{\text{time}} = 0.9051$, and $p_{\text{interaction}} = 0.8642$).

Trends for the Shannon–Wiener diversity index were similar to those for species richness. Calculated diversity values varied from 1.5 to 3.5, and, except in Hibernia Lake, decreased with time (Fig. 2; $F_{[2,27(\text{time})]} = 6.70$, $p = 0.004$). Removing both UV-A and UV-B significantly increased species diversity as assessed by this metric (Fig. 2; $F_{[2,27(\text{UVR})]} = 6.04$, $p = 0.007$; $F_{[4,27(\text{interaction})]} = 1.77$, $p = 0.155$). Although trends for Simpson's diversity index were again similar to those for Shannon-Wiener (Fig. 2), these results were non-significant ($F_{[2,27(\text{UVR})]} = 2.49$, $p = 0.102$; $F_{[2,27(\text{time})]} = 5.53$, $p = 0.010$; $F_{[4,27(\text{interaction})]} = 1.77$, $p = 0.164$).

Algal taxonomy: biomass and community composition

In all lakes, the diatoms were clearly the largest contributor to algal biomass (Fig. 3), with the Cyanobacteria and chlorophytes composing a smaller portion of the total. The relative contribution of non-diatom taxa was much higher in

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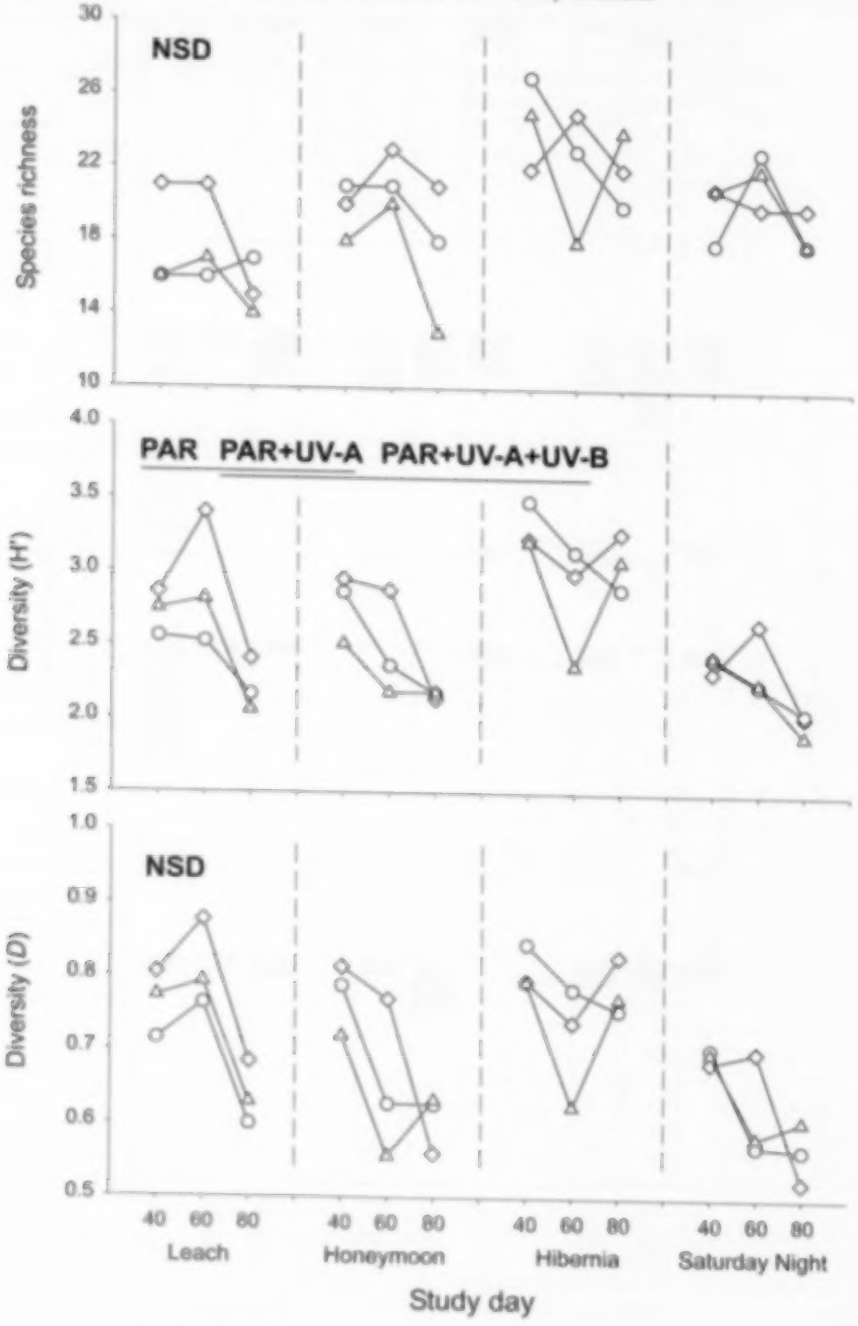
Fig. 2. Species richness and Shannon–Wiener (H') and Simpson's (*D*) diversity indices under three different ultraviolet radiation (UVR) regimes in four study lakes in Jasper National Park, Alberta. Statistical results for two-way analyses of variance comparing the effect of UVR across all lakes within each index are shown. NSD, no significant difference between comparisons; △, photosynthetically active radiation (PAR) + UV-A + UV-B treatment; ○, PAR + UV-A treatment; ◇, PAR-only treatment.



Honeymoon Lake than in the other three study lakes. The algal species identified in our experimental communities are given in Table 1.

Nonstatistical assessment suggests that exposure to UV-A and UV-B did not change the biomass or percent composition of epilithon in the four study lakes (Fig. 3). However, several broad taxonomic shifts were observed. In Honeymoon Lake on the second study date, the chlorophytes *Mougeotia* sp. and *Bulbochaete* sp. increased under the PAR treatment, while the diatoms *Cymbella* sp. and *Navicula rosa*

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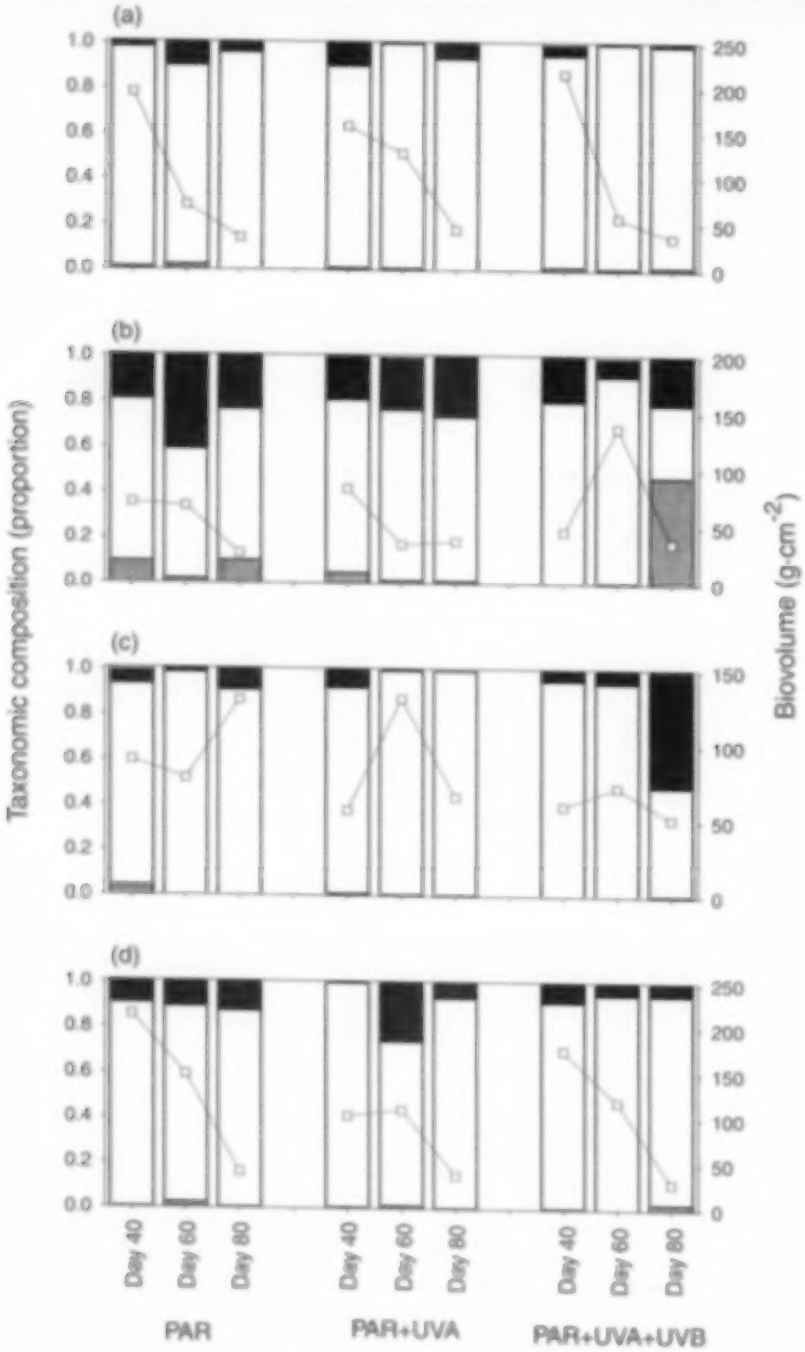
Fig. 3. Algal taxonomic composition and biomass under three different UVR regimes in Leach Lake (*a*), Honeymoon Lake (*b*), Hibernia Lake (*c*), and Saturday Night Lake (*d*) in Jasper National Park, Alberta. Solid bars denote the proportion of chlorophytes; open bars denote the proportion of diatoms; shaded bars denote the proportion of Cyanobacteria; and lines indicate total biovolume.



increased in the PAR + UV-A + UV-B treatment. This increased diatom biomass is largely responsible for the observed increase in total biomass (Fig. 3). In Honeymoon Lake on the last study date, the observed increase in Cyanobacteria biomass under the PAR + UV-A + UV-B treatment is driven by increases in *Scytonema* sp., a genus capable of producing UVR-protectant compounds. In Hibernia Lake, increased chlorophyte volume on the last study date under

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Table 1. Algal taxa in four lakes in Jasper National Park, Alberta.

Cyanobacteria
1. *Aphanothece* sp.
2. *Chroococcus limneticus* Lemmermann
3. *Merismopedia glauca* (Ehrenberg) Kützing
4. *Anabaena* sp.
5. *Phormidium tenue* Anagnostidis and Komarek
6. *Lyngbya* sp.
7. *Cylindrospermum* sp.
8. *Anabaenopsis* sp.
9. Heterocysts
10. *Pseudoanabaena* sp.
11. *Rivularia* sp.
12. *Gloeothece* sp.
13. *Scytonema* sp.

Chlorophytes
14. *Pediastrum duplex* Meyen
15. *Pediastrum tetras* (Ehrenberg) Ralfs
16. *Oocystis borgei* Snow
17. *Scenedesmus quadricauda* (Turp.) Brebisson
18. *Scenedesmus denticulatus* Lagerhiem
19. *Scenedesmus* sp.
20. *Closterium kuetzingii* Brebisson
21. *Cosmarium depressum* v achondrum (Boldt)
22. *Euastrum denticulatum* Gay
23. *Euastrum* spp.
24. *Mougeotia* sp.
25. *Bulbochaete* sp.

Chrysophytes
26. *Kephyrion spirale* (Lackey) Conrad
27. *Dinobryon sertularia* Ehrenberg

Diatoms
28. *Fragilaria construens* v binodis Grunow
29. *Gomphonema constrictum* Ehrenberg
30. *Gomphonema constrictum* v capitata
31. *Cyclotella meneghiniana* Kützing
32. *Cyclotella stelligera* Cleve and Grunow
33. *Tabellaria fenestrata* (Lyngbye) Kützing
34. *Fragilaria crotonensis* Kitton
35. *Fragilaria construens* (Ehrenberg) Grunow
36. *Synedra acus* Khtzing
37. *Synedra ulna* (Nitzsch) Ehrenberg
38. *Gomphonema* sp.
39. *Pinnularia* sp.
40. *Gyrosigma* sp.
41. *Frustulia rhomboides* (Ehrenberg) de Toni
42. *Achnanthes linearis* W. Smith
43. *Achnanthes minutissima* Kützing
44. *Cymbella* sp.
45. *Cyclotella bodanica* Eulenst.
46. *Encocconeis* sp.
47. *Epithemia argus* Kützing
48. *Frustulia vulgaris* Thwaites
49. *Navicula subtilissima* Cleve
50. *Sellaphora pupula* (Kützing) Mereschow
51. *Navicula* sp.
52. *Nitzschia fonticola* Grunow

Table 1 (*concluded*).

53. *Nitzschia linearis* W. Smith
54. *Neidium* sp.
55. *Stauroneis anceps* Ehrenberg
56. *Eunotia* sp.
57. *Brachysira brebissonii* (Ross in Hartley)
58. *Neidium iridis* (Ehrenberg) Cleve
59. *Pinnularia subcapitata* Gregory
60. *Cocconeis* sp.
61. *Rhopalodia* sp. O. Muller
62. *Brachysira exilis* (Kütz.) Cleve
63. *Brachysira follis* (Ehrenberg) R.Ross
64. *Cymbella amphicephala* Naegeli
65. *Fragilaria pinnata* Ehrenberg
66. *Cymbella gracilis* (Rabhorst) Cleve
67. *Cymbella microcephala* Grunow
68. *Cymbella pusilla* Grunow
69. *Surirella linearis* v constricta (Ehrenberg)
70. *Pinnularia borealis* Ehrenberg
71. *Amphora ovalis* Kützing
72. *Nitzschia filiformis* (W. Smith) Hustedt
73. *Diatoma vulgare* Bory
74. *Pinnularia gibba* Ehrenberg
75. *Gomphonema olivaceum* (Lyngbye) Kützing
76. *Diatoma* sp.
77. *Neidium gracile* Hustedt
78. *Navicula bacillum* Ehrenberg
79. *Denticula elegans* Kützing

Dinoflagellate
80. *Peridinium pusillum* (Penard) Lemmermann

Note: Numbers correspond to those used in Fig. 4.

the PAR + UV-A + UV-B treatment is caused by a proliferation of a large-celled *Bulbochaete* species. Overall, however, no trend of increasing cell size with UVR was observed (data not shown).

Multiple environmental factors and algal community structure: ordination analysis

Preliminary investigation of species data by detrended correspondence analysis revealed that the maximum gradient length represented by the canonical axes was less than 3 units of standard deviation, verifying that a linear (RDA) rather than a unimodal response model would best fit our data (maximum length = 2.8; ter Braak and Šmilauer 1998). Preliminary forward selection of all environmental variables resulted in a ranking order of Si, $NO_2^- + NO_3^-$, alkalinity, conductivity, PAR, UV-A, chironomid density, temperature, NH_4^+, TDP, DOC, and UV-B.

Initial screening eliminated redundant variables that did not contribute significantly to the ordination. The variables alkalinity and conductivity were highly correlated ($VIF_{alkalinity}$ = 190.5, $VIF_{conductivity}$ = 179.4); conductivity was removed from the ordination because it was less significant in the initial forward selection. Forward selection in the absence of the variable conductivity further removed PAR, TDP, UV-B, and DOC as variables that did not significantly improve the fit of the model (p = 0.45, 0.53, 0.62, and 0.88, respectively,

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Table 2. Eigenvalues, and their associated significance levels, and cumulative percent variance of the species data explained by the four ordination axes.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.178	0.108	0.064	0.034
p	0.01	0.005	0.025	0.21
Cumulative explanation (%)	17.8	28.6	35.1	38.5
Correlation of environmental variables with axes (r)				
UV-A*	0.084	0.083	0.019	–0.72
Temperature	–0.362	0.049	0.014	0.198
NH_4^+	0.31	–0.49	0.27	0.124
$NO_2^- + NO_3^-$	0.318	–0.523	0.073	0.073
Si concentration	–0.793	–0.291	–0.073	–0.113
Alkalinity	–0.58	–0.353	–0.483	–0.092

Note: Each of the six environmental variables is listed with its r-value correlation with each axis. Values of p are calculated by Monte-Carlo methods with 199 permutations.
*Ultraviolet-A radiation.

Monte-Carlo test with 199 permutations). Chironomid density was finally removed because it exerted a significant skewing effect on several of our sites and was not a significant descriptor of algal distribution when these sites were removed.

The first four axes of RDA with the remaining, significant environmental variables explained 38.5% of the species variance found in these study lakes (Table 2). Concentration of Si and alkalinity were most strongly related to the first canonical axis, which was significant ($p = 0.010$, Monte-Carlo test with 199 permutations) and explained 17.8% of the variance in the species-assemblage data (Table 2, Fig. 4). The second canonical axis was also significant ($p = 0.005$, Monte-Carlo test with 199 permutations) and explained a further 10.8% of the species variance. This axis largely explained an available nitrogen gradient, NH_4^+ and $NO_2^- + NO_3^-$ being its largest contributors (Table 2, Fig. 4).

The first and second canonical axes tend to contrast diatoms with Cyanobacteria and chlorophytes. Not surprisingly, chlorophytes and Cyanobacteria are inversely related to the Si vector. These taxa were most abundant in Honeymoon Lake, where Si concentrations were lowest. Diatoms clustered in a strong negative relationship with the second axis. The diatom species that were most poorly related to the nitrogen vectors arising from this axis (*Epithemia argus*, *Rhopalodia* sp., and *Denticula elegans*) have the ability to form endosymbiotic relationships with nitrogen-fixing Cyanobacteria (Graham and Wilcox 2000). In comparatively nitrogen-rich Honeymoon Lake, these three species were either rare or absent. Despite its removal from our model, total algal biomass was also positively correlated with TDP (biomass = 0.952 + 51.5518·log(TDP), $n = 36$, $r^2 = 0.165$, $p = 0.014$).

The third axis, also significant (Table 2), is again dominated by measures of nutrient status. UV-A is strongly correlated only with axis 4, which does not significantly explain additional variance in the species assemblages. Although variations in nutrient concentration are clearly the largest contributor to species variation in these lakes, an investigation of the fourth ordination axis reveals some patterns in the species data with respect to UVR (Fig. 4). None of the taxonomic groups showed an overall negative correlation with the UV-A vector. However, it was specific chlorophyte (*Mougeotia* sp.) and diatom (*Gomphonema constrictum* and *Synedra acus*) species that were most negatively related to UV-A (Fig. 4; Tank 2002). No species had a strong positive relationship with UV-A. Those that did correlate positively with the UV-A axis (e.g., *Navicula* sp., *Nitzchia linearis*, and *Fragilaria crotonensis*) showed constant biomass across all radiation levels, rather than increases in the presence of UV-A.

Algal pigment composition

In Leach, Honeymoon, and Saturday Night lakes, there was an overall trend for algal carotenoid and chlorophyll concentrations to decrease over time, while in Hibernia Lake concentrations increased (Fig. 5, Tables 3 and 4). In the carotenoids, within-lake responses to UVR manipulations were similar across all pigment types (Table 3). In Leach Lake, exposure to both UV-A and UV-B led to significant decreases in carotenoid concentrations (Fig. 5, Table 3). In Honeymoon Lake, carotenoids were again reduced in the presence of UVR, although there was a strong interaction with time, caused by a dip in carotenoid concentrations under the PAR treatment on the second sampling occasion (Fig. 5, Table 3). Although MANOVA contrasts suggest that carotenoid concentrations tended to be higher in the PAR treatment ($p = 0.027$), this effect was not significant at the Dunn–Šidák-adjusted p value (Fig. 5, Table 3). In Hibernia Lake, the effect of light treatment on carotenoid concentrations showed no significant, common pattern (MANOVA; Fig. 5, Table 3). However, fucoxanthin concentrations were significantly higher under the PAR + UV-A treatment (Table 3, Tukey–Kramer test). In Saturday Night Lake, carotenoids decreased in the presence of UVR (MANOVA; Fig. 5, Table 3). However, as in Honeymoon Lake, although MANOVA contrasts suggest that carotenoid concentrations were suppressed under UV-A + UV-B exposure ($p = 0.022$), this effect was not significant at the Dunn–Šidák-adjusted p value.

The trends in the chlorophyll pigments were much less pronounced than those in the carotenoids. In Leach Lake, chlorophyll concentrations decreased significantly with combined exposure to UV-A and UV-B (Fig. 5, Table 4). In Honeymoon Lake, although pheophytin *a* concentrations de-

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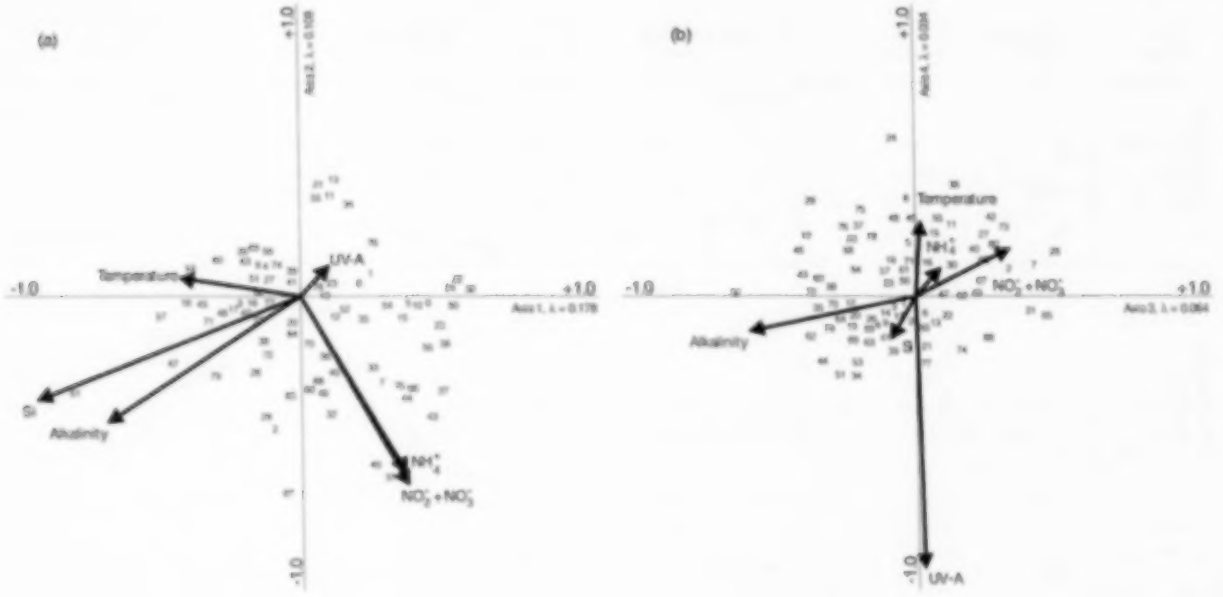
Fig. 4. Correlation biplots of algal species and environmental variables in four lakes in Jasper National Park, Alberta. Axes 1 and 2 (*a*) and axes 3 and 4 (*b*) of the redundancy analysis are shown. Numbers correspond to algal taxa given in Table 1.



creased significantly under UV-B exposure (Table 4; Tukey–Kramer test). MANOVA indicates no significant overall effect of UVR exposure on chlorophyll concentrations (Fig. 5, Table 4). No other significant effects of UVR on chlorophyll concentrations were observed (Fig. 5, Table 4).

Algal pigment ratios

The ratio of carotenoids to chlorophyll *a* decreased significantly with UVR exposure in Honeymoon, Hibernia, and Saturday Night lakes (MANOVA; Fig. 5, Table 5). This change was driven by decreases in the relative concentrations of β-carotene in Honeymoon and Hibernia lakes, fucoxanthin in Hibernia and Saturday Night lakes, and violaxanthin in Saturday Night Lake (Table 5). In Honeymoon and Saturday Night lakes, this ratio appears to be greatest in the PAR treatment, while in Hibernia Lake, ratios in the PAR + UV-A treatment are greater than in the PAR + UV-A + UV-B treatment (Fig. 5, Table 5). Although this general trend also occurs in Leach Lake, the result is not statistically significant (Fig. 5, Table 5).

Discussion

The role of UVR in structuring epilithic communities

Our results suggest that UVR may not be of primary importance in controlling algal taxonomy, total biomass, and distribution in the epilithon of montane lakes. In our study, we found no consistent taxonomic shifts between the major taxonomic groups under differential UVR exposure, and no overall biomass response to UVR. Decreases in algal biomass with UVR exposure have often been observed in both attached and planktonic communities (e.g., Worrest et al. 1981; Vinebrooke and Leavitt 1996). However, some studies have shown UVR to be unimportant (Vinebrooke and Leavitt 1998) or of secondary importance (e.g., Xenopoulos et al. 2002) in structuring these communities.

In our experimental communities, ordination analysis suggests that nutrient concentrations, and not light quality, are most important for structuring epilithic assemblages. Such strong correlations between nutrients and algal biomass are not unexpected in these oligotrophic systems: concentrations of both nitrogen and phosphorus were low in our study lakes. Molar epilithic C:P ratios ≥600 and C:N ratios as high as 20 further suggest that algae of the epilithon are highly nutrient-limited in these lakes (Tank et al. 2003). In fact, nutrient limitation could be the cause of the poor response to UVR in our study communities. Several studies have shown the presence of nutrient stress to preclude strong inhibition by UVR in planktonic algae (Behrenfield et al. 1994; Xenopoulos et al. 2002). Other benthic investigations have shown the abundance of species of the nitrogen-fixing Epithemiaceae, such as the endosymbiotic hosts observed in our study, to be strongly inhibited by UVR, despite otherwise weak UVR re-

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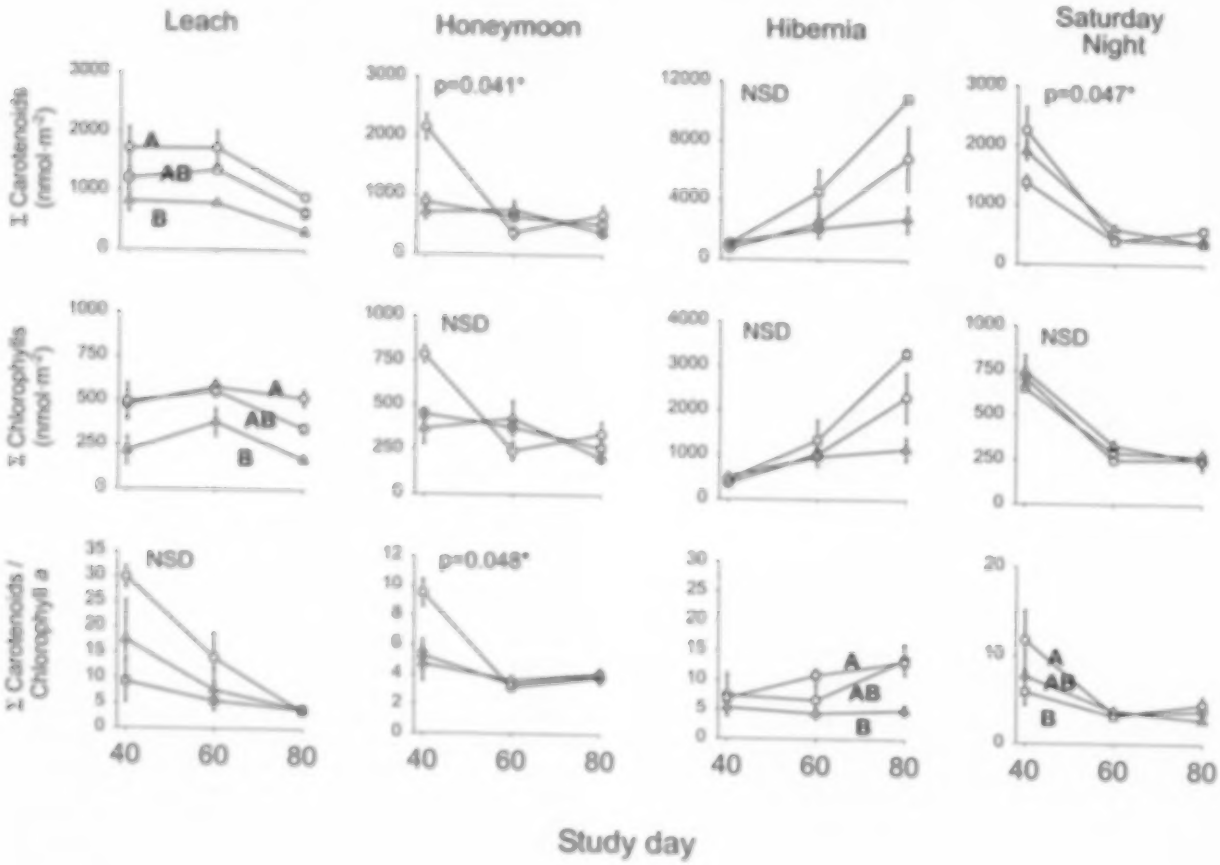
Fig. 5. Mean molar concentrations (mean ± 1 standard error, $n = 2$) of total carotenoid, total chlorophyll, and total carotenoid to chlorophyll *a* ratios under three different UVR regimes in four study lakes in Jasper National Park, Alberta. Significantly different multivariate analysis of variance (MANOVA) contrasts within each panel are indicated using different letters. NSD, no significant difference between comparisons; △, PAR + UV-A + UV-B treatment; □, PAR + UV-A treatment; ○, PAR-only treatment. An asterisk (*) indicates a significant MANOVA result, where post-hoc contrasts are not significant at a Dunn–Šidák-adjusted p value of 0.01.



sponses in the algal community as a whole (Francoeur and Lowe 1998; Watkins et al. 2001). We did not find such a response in our study. However, these species were most abundant in our more coloured lakes, where penetration of UVR to the depth of our experimental incubations may not have been substantial enough to effect such taxonomic shifts.

The epilithic algae of our study lakes did exhibit some minor inhibition in the presence of UVR, suggesting that light quality may indeed have represented a secondary stress in these systems. Combined exposure to both UV-A and UV-B decreased algal diversity, as assessed by the Shannon–Wiener index. In addition, closer investigation of our ordination analysis indicated that subtle, species-specific shifts might have occurred as a result of UVR exposure. Several species were found to have reduced biomass in the presence of UV-A. Of these, *Mougeotia* sp. was the most strongly inhibited. This species is traditionally expected to increase in the presence of UVR: it has been found to increase to large numbers in acidified lakes (Turner et al. 1995), where acid-mediated bleaching of DOC causes substantial increases in water clarity (Schindler and Curtis 1997). Other studies, however, have also found decreased *Mougeotia* sp. biomass in response to UVR exposure (Kaczmarska et al. 2000).

Although the biomass of diatoms as a whole did not decrease with exposure to UVR, both *G. constrictum* and *S. acus* decreased with increasing UV-A, suggesting that certain diatoms in our study communities displayed increased sensitivity to UVR. Other species of these genera have been found to increase in the absence of UVR (Vinebrooke and Leavitt 1996; Francoeur and Lowe 1998). *Synedra acus* is a small organism (~100 μm³), which may have led it to be more susceptible to UVR exposure (Garcia-Pichel 1994). Furthermore, *S. acus* has an upright aspect, while *Gomphonema* sp. is often stalked (Graham and Wilcox 2000). These traits are also indicative of UVR susceptibility because of decreased shading of those species that may extend above the epilithic matrix (Vinebrooke and Leavitt 1998). In contrast, *Achnanthes minutissima* did not respond to UV-A in this study, despite previous findings that this spe-

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Table 3. Multivariate and two-way analysis of variance (MANOVA and two-way ANOVA) results for the effects of ultraviolet radiation (UVR) on log-transformed taxon-specific carotenoid concentrations in four study lakes in Jasper National Park, Alberta.

		Leach Lake		Honeymoon Lake		Hibernia Lake		Saturday Night Lake	
	df	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Canthaxanthin[a]									
UVR	2	27.89	**0.0001**	9.17	**0.007**	5.71	0.025	1.37	0.303
Time	2	11.36	**0.004**	20.72	**0.0004**	34.05	**<0.0001**	5.00	**0.035**
UVR × time	4	1.17	0.387	8.01	**0.005**	1.96	0.184	6.49	**0.010**
Diatoxanthin[a]									
UVR	2	18.91	**0.001**	3.46	0.077	4.02	0.057	1.28	0.324
Time	2	11.40	**0.003**	11.00	**0.004**	20.56	**0.0004**	115.50	**<0.0001**
UVR × time	4	0.32	0.860	7.24	**0.007**	2.35	0.132	4.28	0.033
Echinenone[a]									
UVR	2	14.49	**0.002**	7.87	0.011	4.41	0.046	1.01	0.401
Time	2	4.84	0.037	9.69	**0.006**	44.82	**<0.0001**	3.33	0.083
UVR × time	4	0.98	0.464	4.61	**0.027**	2.49	0.118	1.78	0.218
Fucoxanthin[a]									
UVR	2	12.9430	**0.0022**	0.72	0.515	8.70	**0.008**[b]	0.14	0.867
Time	2	19.4526	**0.0005**	19.64	**0.0005**	53.41	**<0.0001**	171.38	**<0.0001**
UVR × time	4	0.4168	0.7928	7.67	**0.006**	3.03	0.077	7.61	**0.006**
Violaxanthin[a]									
UVR	2	24.91	**0.0002**	1.05	0.390	0.11	0.896	1.66	0.244
Time	2	27.45	**0.0001**	12.52	**0.003**	19.82	**0.0005**	18.27	**0.001**
UVR × time	4	1.03	0.4409	2.26	0.143	1.71	0.231	5.72	0.014
MANOVA									
UVR	2	6.91	**0.0060**	3.59	**0.041**	2.64	0.091	3.43	**0.047**
Time	2	6.01	**0.009**	10.63	**0.001**	10.33	**0.002**	307.65	**<0.0001**
UVR × time	4	0.93	0.567	4.79	**0.002**	1.08	0.453	5.48	**0.001**

Note: Degrees of freedom, *F* statistics, and *p* values are reported for $n = 2$ replicates. Results significant at an adjusted *p* value of 0.0102 for two-way ANOVAs and a *p* value of 0.05 for MANOVA are in boldface type. The Hotelling–Lawley *F* statistic was used in the MANOVA test. Where ANOVA, but not MANOVA, showed a significant UVR response within lakes, the Tukey–Kramer test was performed on individual ANOVA results. PAR, photosynthetically active radiation; UV-A, ultraviolet-A radiation; UV-B, ultraviolet-B radiation.

[a]'Pigments' representative taxa, modified from Millie et al. (1993), are as follows: canthaxanthin: Cyanobacteria; diatoxanthin: diatoms; echinenone: Cyanobacteria; fucoxanthin: diatoms, chrysophytes; violaxanthin: chlorophytes.

[b]Tukey–Kramer test: PAR PAR + UV-A PAR + UV-A + UV-B ($p < 0.05$).

cies tends to decline strongly under UVR stress (e.g., Vinebrooke and Leavitt 1996).

In our ordination analysis, neither UV-B nor PAR was found to be a significant predictor of algal biomass and distribution. Although UV-B is potentially more damaging than UV-A, fluxes of UV-B to the benthos may have been too low to be of significance, owing to low solar influx and high attenuation of UV-B in the water column (Cullen and Neale 1994). Other studies have shown UV-A to be the major photoinhibitor of algal populations (e.g., Milot-Roy and Vincent 1994), while models of UVR-induced damage in the phytoplankton predict that UV-B should be of minor importance because of low fluxes in the UV-B range (Cullen and Neale 1994). The exclusion of PAR from our model may simply indicate that our systems were not light-limited. However, this result may also have been caused by the strong correlation between PAR and temperature, which was included in our model.

The effect of UVR on epilithic pigments

In contrast to the insignificant response observed for our count-based estimates of algal biomass, epilithic pigment concentrations were markedly depressed in the presence of UV-A and UV-B. The decrease was much more striking for carotenoid concentrations than for the chlorophylls, and as a result, carotenoid to chlorophyll *a* ratios also decreased under UVR exposure.

Although photosynthetic pigments are often used as biomass indicators (Millie et al. 1993), UVR has been shown to alter the pigment content of algal cells. Under intense short-term exposure, UVR can reduce cellular algal carotenoid and chlorophyll concentrations (e.g., Döhler and Buchmann 1995). However, carotenoids are important photoprotective compounds (Roy 2000). In contrast to our results, long-term studies generally show increases in carotenoids, or in carotenoid to chlorophyll ratios, in chronically UVR-stressed algal cells (e.g., Paerl et al. 1983; Goes et al. 1994).

There are several potential explanations for (*i*) the discrepancy between the observed pigment results and algal biomass counts, and (*ii*) the atypical response of cellular pigment concentrations to UVR exposure in this study. First, the pigment results could indicate biomass increases in our UVR-shielded algal communities that were not mirrored in the taxonomic data because of incorrect or highly variable

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Table 4. MANOVA and two-way ANOVA results for the effects of UVR on log-transformed chlorophyll concentrations in four study lakes in Jasper National Park, Alberta.

		Leach Lake		Honeymoon Lake		Hibernia Lake		Saturday Night Lake	
	df	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Chlorophyll *a*[a]									
UVR	2	4.09	0.054	0.13	0.872	1.19	0.349	2.82	0.112
Time	2	6.34	0.019	1.07	0.382	16.23	**0.001**	8.18	**0.009**
UVR × time	4	1.52	0.276	1.10	0.412	0.47	0.759	0.27	0.890
Chlorophyll *b*[a]									
UVR	2	4.76	0.039	3.08	0.096	0.73	0.508	0.39	0.686
Time	2	4.30	0.049	11.30	0.004	20.85	0.0004	1.87	0.209
UVR × time	4	0.99	0.459	3.99	0.039	0.71	0.608	1.29	0.344
Chlorophyll *c*[a]									
UVR	2	5.38	0.030	0.78	0.487	5.41	0.029	2.41	0.145
Time	2	2.02	0.189	2.03	0.187	12.03	**0.003**	52.13	**<0.0001**
UVR × time	4	1.45	0.294	2.45	0.122	8.75	**0.004**	4.70	0.025
Pheophytin *a*[a]									
UVR	2	14.40	**0.002**	10.14	**0.005**[b]	6.28	0.02	0.13	0.877
Time	2	24.08	**0.0002**	131.95	**<0.0001**	15.55	**0.001**	24.84	**0.0002**
UVR × time	4	0.80	0.557	5.34	0.018	0.80	0.557	1.17	0.387
MANOVA									
UVR	2	4.65	**0.013**	1.97	0.156	2.41	0.097	0.78	0.633
Time	2	5.16	**0.009**	21.62	**<0.0001**	5.73	**0.006**	27.04	**<0.0001**
UVR × time	4	0.54	0.888	1.41	0.238	1.74	0.128	1.60	0.169

Note: Degrees of freedom, *F* statistics, and *p* values are reported for $n = 2$ replicates. Results significant at an adjusted *p* value of 0.0127 for two-way ANOVAs and a *p* value of 0.05 for MANOVA are in boldface type. The Hotelling–Lawley *F* statistic is used in the MANOVA test. Where ANOVA, but not MANOVA, showed a significant UVR response within lakes, the Tukey–Kramer test was performed on individual ANOVA results.
[a]"Pigments" representative taxa, modified from Millie et al. (1993), are as follows: chlorophyll *a*: all algae; chlorophyll *b*: chlorophytes; chlorophyll *c*: diatoms, chrysophytes; pheophytin *a*: all algae, degradation product.
[b]Tukey–Kramer test: PAR PAR + UV-A PAR + UV-A + UV-B ($p < 0.05$).

counts. This explanation seems unlikely. Increased algal biomass in UVR-shielded communities would likely not result in increases in carotenoid concentrations only, with chlorophyll concentrations remaining relatively constant. Furthermore, during algal counts care was taken to only count live cells (Owen et al. 1978). Similarly, although pico-plankton-sized cells are easily missed in algal counts, we have found no report of these cells in the benthos. Thus, errors or variability due to missed or wrongly counted cells were likely rare.

An UVR-specific shift of intercellular algal pigment concentrations is a second possible explanation for our observations. Again, this seems unlikely. In chlorophytes and Cyanobacteria, carotenoid concentrations have been documented to increase in response to acute UVR exposure (Roy 2000), while photobleaching of chlorophylls is known to result in increased carotenoid to chlorophyll ratios under UVR stress (Vernet 2000). The universal decrease in carotenoid concentrations and carotenoid to chlorophyll ratios that we observed under UVR exposure is unexpected at the cellular level.

Clearly, the results of our study are in contrast to those in which increased concentrations of photoprotective carotenoids have been found in UVR-exposed communities. Unlike our study, most have been carried out in the pelagic zone, where grazed cells quickly sediment out of the water column (Carpenter et al. 1986), or in simplified ex-situ benthic communities, where the influence of grazers is negligible or absent. We propose that in the in-situ benthic communities of our study, grazing and the accumulation of detrital material decoupled measures of pigment and biomass accrual.

In our study communities, the abundance of invertebrate grazers increased in UVR-shielded communities (Tank et al. 2003). When grazed, carotenoids have been shown to be much more resistant to degradation than chlorophylls (Poister et al. 1999). Chlorophylls, conversely, undergo extensive photobleaching once senescence occurs (e.g., Carpenter et al. 1986). Thus, high grazing pressure might be expected to increase carotenoid to chlorophyll ratios, through dissimilar degradation rates of these pigments in grazed cells. We suggest that the elevated carotenoid concentrations observed in our UVR-shielded communities are an artifact of increased algal growth in the absence of UVR, and that this increased growth was counterbalanced by increased grazing pressure. This imbalance between measures of pigment and algal-biomass accrual suggests the need for caution when using pigment-based estimates of algal biomass and taxonomic composition in the benthos.

In our study of four montane lakes, we found little effect of UVR on algal-community composition. Species diversity, but not richness, was altered and of our 80 observed algal species, 3 decreased significantly under UVR exposure. Algal pigments, however, did decrease under UVR stress. Although analyses of photosynthetic pigments do suggest a

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Table 5. MANOVA and two-way ANOVA results for the effects of UVR on carotenoid to chlorophyll *a* ratios in four study lakes in Jasper National Park, Alberta.

		Leach Lake		Honeymoon Lake		Hibernia Lake		Saturday Night Lake	
	df	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
β-carotene: chlorophyll *a*[a]									
UVR	2	1.94	0.199	5.73	0.025	11.8	**0.003**	0.10	0.906
Time	2	9.67	**0.006**	7.12	0.014	4.12	0.054	4.26	0.050
UVR × time	4	0.72	0.601	3.18	0.069	0.79	0.560	0.30	0.868
Diatoxanthin: chlorophyll *a*[a]									
UVR	2	1.80	0.220	1.93	0.200	3.11	0.094	1.60	0.255
Time	2	7.78	**0.011**	12.20	**0.003**	0.29	0.756	40.16	**<0.0001**
UVR × time	4	0.72	0.599	2.26	0.142	0.94	0.483	4.38	0.031
Fucoxanthin: chlorophyll *a*[a]									
UVR	2	0.48	0.633	0.16	0.851	3.91	0.060	6.51	**0.004**
Time	2	17.62	**0.001**	13.05	**0.002**	1.62	0.250	20.45	**<0.0001**
UVR × time	4	1.23	0.364	3.28	0.064	0.59	0.676	7.55	**<0.0001**
Violaxanthin: chlorophyll *a*[a]									
UVR	2	4.22	0.051	0.25	0.784	1.54	0.267	9.30	**0.007**
Time	2	30.10	**0.0001**	26.48	**0.0002**	0.94	0.426	10.02	**0.005**
UVR × time	4	0.67	0.630	0.46	0.764	1.35	0.324	10.85	**0.002**
MANOVA									
UVR	2	2.54	0.085	3.12	**0.048**	4.10	**0.021**	6.51	**0.004**
Time	2	8.36	**0.002**	6.39	**0.004**	2.66	0.075	20.45	**<0.0001**
UVR × time	4	1.61	0.164	2.34	**0.042**	0.91	0.572	7.55	**<0.0001**

Note: Degrees of freedom, *F* statistics, and *p* values are reported for $n = 2$ replicates. Results significant at an adjusted *p* value of 0.0127 for two-way ANOVAs and a *p* value of 0.05 for MANOVA are in boldface type. The Hotelling–Lawley *F* statistic is used in the MANOVA test.

[a]'Pigments' representative taxa, modified from Millie et al. (1993), are as follows: chlorophyll *a*: all algae; β-carotene: all algae; diatoxanthin: diatoms; fucoxanthin: diatoms, chrysophytes; violaxanthin: chlorophytes.

certain amount of sensitivity to UVR in our benthic systems, it appears that nutrients and grazers are much more important in structuring these epilithic algal communities than variations in light quality.

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Availability to Steller sea lions (*Eumetopias jubatus*) of a seasonal prey resource: a prespawning aggregation of eulachon (*Thaleichthys pacificus*)

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Abstract: The availability of seasonally abundant energy-rich prey can be a significant factor for the survival and reproductive success of predator populations. Large numbers of Steller sea lions (*Eumetopias jubatus*) were attracted to a prespawning aggregation of eulachon (*Thaleichthys pacificus*) in Berners Bay in southeast Alaska during April–May in 2002 and 2003. Sea lion abundance increased as eulachon gathered in Berners Bay, peaked as eulachon abundance peaked, and decreased as the eulachon moved up-river. As sea lion abundance increased in Berners Bay, sea lion abundance decreased at Benjamin Island, a sea lion haulout located 22 km away. The eulachon provided an abundant, energy-rich, predictable prey source for the Steller sea lions: (*i*) eulachon energy density was 9.70 ± 0.24 kJ·g^{-1}, much higher than that of any forage species reported in the North Pacific Ocean except northern lampfish (*Stenobrachius leucopsarus*); (*ii*) a large surplus of prey was available per sea lion while the eulachon aggregation was present; and (*iii*) the spawning run usually begins between late April and early May. The eulachon pulse may be critical to Steller sea lions during a period of high energetic demands.

Résumé : La disponibilité de proies riches en énergie à certaines périodes de l'année peut être un facteur significatif pour la survie et le succès reproductif des populations de prédateurs. Un grand nombre de lions de mer de Steller (*Eumetopias jubatus*) ont été attirés par des rassemblements préparatoires à la fraye d'eulakanes (*Thaleichthys pacificus*) dans la baie de Berners dans le sud-est de l'Alaska en avril et en mai 2002 et 2003. L'abondance des lions de mer s'est accrue à mesure que les eulakanes se rassemblaient dans la baie de Berners, elle a atteint un sommet en même temps que celle des eulakanes et elle a décru lorsque les eulakanes se sont déplacés vers l'amont de la rivière. À mesure que l'abondance des lions de mer augmentait à la baie de Berners, elle diminuait à l'île Benjamin, une échourie pour les lions de mer située à 22 km. Les eulakanes représentent pour les lions de mer de Steller une source de proies abondantes, riches en énergie et prévisibles : (*i*) la densité énergétique des eulakanes est de 9,70 ± 0,24 kJ·g^{-1}, une valeur bien supérieure à celle de tout autre poisson fourrage du Pacifique nord, sauf la lanterne du nord (*Stenobrachius leucosparus*); (*ii*) durant le rassemblement des eulakanes, il y a un surplus considérable de proies disponibles pour chacun des lions de mer; et (*iii*) la migration de fraye commence généralement à fin d'avril ou au début de mai. Ce foisonnement d'eulakanes peut être d'importance critique pour les lions de mer de Steller à un moment où leurs besoins énergétiques sont grands.

[Traduit par la Rédaction]

Introduction

Ecosystems tend to develop components that maximize utilization of seasonally available energy pulses (Odum et al. 1995). Marine examples are anadromous fishes such as salmon (*Oncorhynchus* spp.; Willson and Halupka 1995) and eulachon (*Thaleichthys pacificus*; Marston et al. 2002), whose spawning aggregations provide important seasonal food resources for mammalian and avian predators. The salmon pulse is characterized by prey that is temporarily very abundant, spatially constrained, relatively easy to capture, and more or less spatiotemporally predictable (Willson and Halupka 1995). Eulachon are energy-rich (Iverson et al. 2002) and concentrate in shallow waters along the river margins during spawning (Marston et al. 2002). However, eulachon is not a commercially harvested species and therefore

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little is known about eulachon ecology, except for a description of predator–prey interactions in southeast Alaska (Gende et al. 2001; Marston et al. 2002).

Eulachon are anadromous smelt (Osmeridae) that spawn primarily in mainland glacial rivers from California to Alaska (Hart 1973). In southeast Alaska, eulachon typically spawn from March to May and attract large numbers of avian and marine mammal predators (Marston et al. 2002; Womble 2003). One of the predators of eulachon is the Steller sea lion (*Eumetopias jubatus*), which has declined by more than 80% in the western stock since the 1960s (Loughlin et al. 1992; Trites and Larkin 1996). In contrast to the western stock, the eastern stock has increased by 1%–2% per year since the late 1970s and is thought to be near its historical peak in abundance (Calkins et al. 1999).

One explanation for the decline is that sea lions were nutritionally stressed as a result of decreases in quantity and (or) quality of prey species (Trites and Donnelly 2003). Sea lions in the area of decline fed on walleye pollock (*Theragra chalcogramma*) and Atka mackerel (*Pleurogrammus monopterygius*), whereas sea lions in stable areas fed on a more diverse diet, including forage fish species such as Pacific herring (*Clupea pallasii*). Area-specific diet diversity and population change of Steller sea lions may be related, with faster population declines in areas of lower diet diversity (Merrick et al. 1997).

Prey-consumption patterns indicate that Steller sea lions target prey that are densely schooled in spawning or migratory aggregations (Sinclair and Zeppelin 2002). However, most diet studies have been conducted primarily during the breeding season of sea lions and therefore do not measure the importance of seasonally aggregated prey species, such as eulachon, that spawn outside of the breeding season.

The exploitation of eulachon by Steller sea lions may be of substantial seasonal significance to the energy budget of sea lions because eulachon are energy-rich (Iverson et al. 2002) and their spawning aggregations occur during spring, a period of high energetic demands for Steller sea lions (Winship et al. 2002). Previous studies have described aggregations of sea lions and other predators in response to eulachon spawning runs (Gende et al. 2001; Marston et al. 2002; Womble 2003); however, eulachon biomass and energy content available to sea lions has not been quantified in the estuary where predation by sea lions occurs. Therefore, our objectives are (*i*) to quantify the biomass of eulachon and their period of availability, (*ii*) to document the abundance of sea lions in Berners Bay and at nearby haulouts, (*iii*) to measure the energy content of the prespawning aggregations of eulachon available to Steller sea lions, and (*iv*) to further characterize the features of the eulachon pulse beyond those described by Marston et al. (2002).

Methods

Study site

The study was conducted from April to May in 2002 and 2003 in Berners Bay in southeast Alaska (Fig. 1). Berners Bay is fed by two glacial rivers, the Antler and the Lace, and a clearwater river, the Berners, which support spawning runs of eulachon in late April and early May (Marston et al. 2002). A submarine gully of about 100 m water depth is located in the northern part of Berners Bay, where the rivers enter the bay. During preliminary fieldwork in April–May 2001, we found eulachon in the western and northern parts of Berners Bay. In the northern part, they were found in the submarine gully.

Eulachon-abundance surveys

Acoustic data were collected to estimate eulachon abundance. Weekly surveys were conducted in the western and northern parts of Berners Bay. In addition, daily surveys were conducted between 15 and 18 April 2003 and replicate surveys were conducted between 16 and 18 April 2003. In 2002, transects were parallel and oriented from west to east; in 2003, transects followed a zigzag pattern. Transects were spaced 0.8 km apart in the western part and 0.4 km apart in the northern part. Sampling was more intense in the northern part of the bay because eulachon were more abundant there in 2001. Using sea lion activity as an indicator of the location of eulachon prespawning aggregations, the sampling scheme for assessing eulachon biomass was comprehensive enough to estimate eulachon abundance for the entire bay because sea lion foraging was observed only in the western and northern parts of the bay in all of our study years (2001–2003) as well as the years of previous studies (1996–1998) (J. Womble, unpublished data). Acoustic data were collected using a portable 38-kHz Simrad EK60 echo-integration system with a 12° beam angle and stored on disk. The echosounder transducer was towed beside the 11-m F/V *Williwaw* at 11 km·h^{-1}. Location data from a global positioning system (GPS) were collected simultaneously.

Length and weight data and a species-classification scheme for the acoustic data are necessary complements to acoustic data. Length and weight data for prespawning eulachon were collected on (*i*) 27–28 March 2002 outside Berners Bay with a midwater trawl deployed from the 18-m F/V *Solstice*, (*ii*) 23 and 29 April 2002 in Berners Bay with a gillnet deployed from the F/V *Williwaw*, and (*iii*) 1–15 May 2002 in the Antler River with dip nets and 8 April 2003 in Berners Bay with a midwater trawl deployed from the 31-m F/V *Viking Storm*. In 2002, the midwater trawl was a 164 Nordic rope trawl with 1.5-m^2 alloy doors, 7-m height, and 17-m width with a 19 mm mesh codend liner. The midwater trawl was larger in 2003 to match the larger vessel and trawl-handling equipment used that year. In 2003, the midwater trawl was a mesh-wing 25/21/64 trawl with 3.0-m^2 alloy doors, 11-m height, and 29-m width with a 32 mm mesh codend liner. The gillnet was 27.5 m long and 2.4 m wide with five panels of 13-, 19-, 25-, 38-, and 51-mm stretched mesh oriented vertically to sample from the sea floor up into the water column. The dip nets were 31 cm deep with a 31 cm × 31 cm opening and 5-mm mesh, attached to a telescoping 5-m pole.

Different species typically show different acoustic patterns, appearing as single targets or schools with characteristic school shapes and at characteristic water depths. Schools of eulachon were identified with a remotely operated vehicle (ROV) in 2001, with a gillnet in 2002, and with a midwater trawl in 2003. The schools appeared monospecific, as no other species besides eulachon were observed by ROV or

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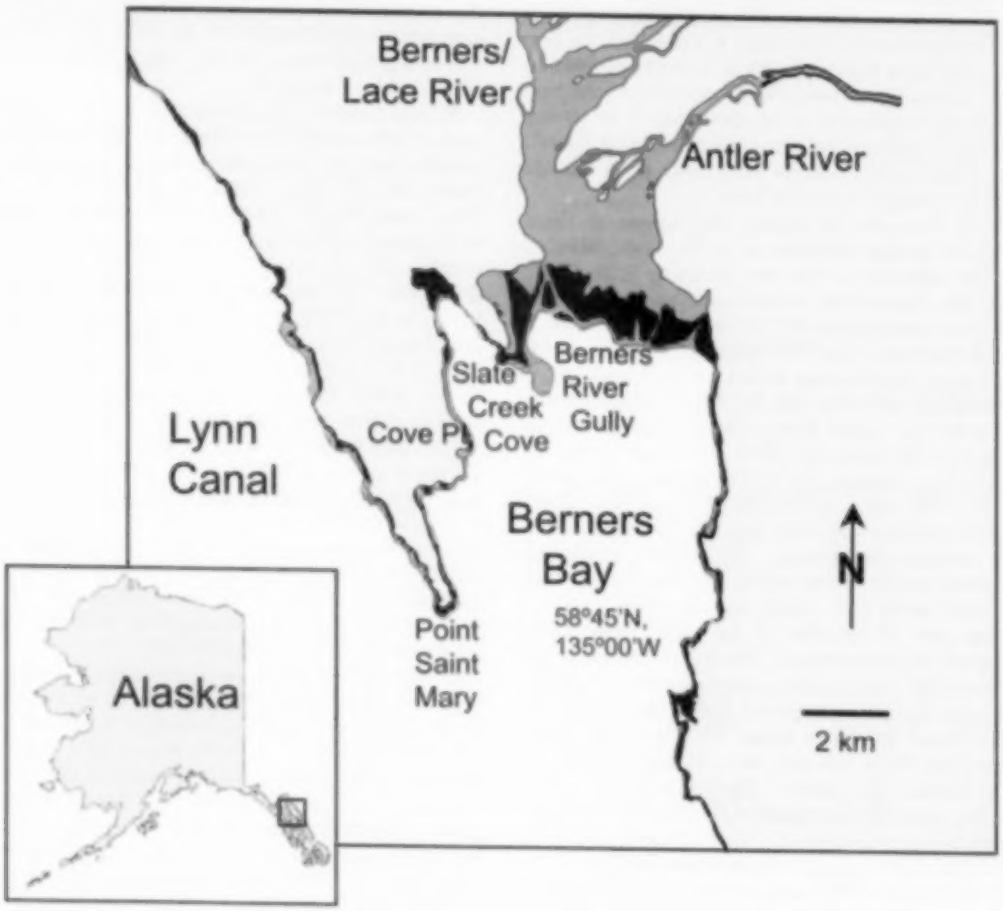
Fig. 1. Study area in Berners Bay, Alaska, USA, a marine bay of about 50 km^2 located 57 km north of Juneau in southeast Alaska (58°45′N, 135°00′W). The dark-shaded areas along the coastline are tidal areas. The boundary of the medium-shaded areas is the 5 m depth contour.



caught by gillnets and nearly all (92% by weight) of the midwater trawl catch was eulachon. Using the corresponding acoustic data, we found that prespawning eulachon schools had diffused rounded edges. The eulachon typically were aggregated into one or two schools. Their acoustic scattering strength was low (the nautical area scattering coefficient (NASC) averaged 76 m^2·naut.mi^{-2}) because eulachon lack a gas bladder (personal communication, S. Gauthier, School of Fishery and Aquatic Sciences, University of Washington, Seattle, WA 98195-5020, USA). These characteristics were used to classify the acoustic data attributable to eulachon because not all eulachon schools were sampled by ROV, gillnet, or midwater trawl.

An echo-integrator summed the returning echoes from fish observed beneath the vessel. The acoustic data were classified by species, integrated for 0.183-km length intervals and 10-m depth intervals, and corrected for instrument calibration using the echo-integration software SonarData Echoview. The output of acoustic scattering (nautical area scattering coefficient (NASC)) is proportional to fish density (MacLennan and Simmonds 1992). To convert NASC to eulachon density in numbers, estimates of acoustic reflectivity for single eulachon were needed. Target strength (TS) refers to the acoustic reflectivity of a single fish and depends on length (L) in centimetres: $TS = 20\log_{10}L + b$ (MacLennan and Simmonds 1992). For eulachon in seawater, $b = -81$ (personal communication, S. Gauthier, School of Fishery and Aquatic Sciences, University of Washington, Seattle, WA 98195–5020, USA). TS is transformed to backscattering cross-section, $\sigma_{bs} = 4\pi 10^{TS/10}$. Eulachon density in numbers was computed by dividing NASC by σ_{bs}. Eulachon density in weight equals density in number multiplied by average weight.

The acoustic data were stratified into three areas: Point Saint Mary (to Cove Point), Slate Creek Cove, and Berners River Gully, which lie southwest, northwest, and northeast of 58°45.27′N, 134°59.210′W (Fig. 1). The sizes of the three areas are 5.5, 4.2, and 2.0 km^2, respectively. Biomass for each area was computed by multiplying eulachon density in weight by the corresponding area size. Total biomass was computed by summing biomass by area.

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Steller sea lion abundance and distribution surveys

Aerial surveys were conducted to estimate Steller sea lion abundance and distribution in the water in Berners Bay and at haulouts in Lynn Canal that were located close to Berners Bay. Aerial surveys were initiated on 8 April 2002 (n = 4 surveys) and 2003 (n = 4 surveys). Most surveys occurred simultaneously with acoustic sampling of eulachon in the bay. Aerial surveys were conducted at approximately 7- to 10-day intervals between 1000 and 1400 using a fixed-wing aircraft (amphibious Cessna 206). Surveys were flown at an altitude of 316 m and a speed of 183–210 km·h^{-1}.

Aerial-survey transects of Berners Bay began at Point Saint Mary at the western terminus of the bay and continued along the entire shoreline of the bay including Slate Creek Cove and the tidal flats of the Berners/Lace and Antler river systems. We flew transects parallel to the shoreline and deviated from the transects when we detected sea lions away from the shoreline. The resultant survey counted sea lions in the water throughout the entire bay. Digital photographic images of sea lions were taken using a digital camera (Nikon D1X) with a telephoto lens (80–300 mm). Small groups of sea lions (<10) were counted and no photographs were taken. Larger groups (>10) were circled and photographed. Overlapping photos were taken if more than one photograph was necessary to complete the coverage. The majority of the sea lion groups were resting at the surface; however, when sea lion groups were active (i.e., diving and surfacing), we circled the group until all members of the group were at the surface and could be photographed. The bay is small enough that all groups of sea lions present presumably were spotted.

Aerial surveys also were conducted at three sea lion haulouts in Lynn Canal. Benjamin Island (22 km), Met Point (33 km), and Gran Point (54 km) are haulouts that are located close to Berners Bay, and it is likely that sea lions that use Berners Bay also use these haulout sites when not foraging in the bay.

The date, time, GPS location, frame numbers, and estimate of sea lion numbers were recorded for all sea lions that were encountered at Berners Bay and at haulouts. Digital photographic images were stored on Lexar Media compact flash cards and then later downloaded to a computer. The clearest digital image was imported into the geographic information system software ArcView®, and each sea lion was marked and the marks were counted. Mark assignments were checked and counted twice by an experienced counter.

The variability of the sea lion counts was not measured, as only one survey was flown each day.

Measurement of eulachon energy content

Analytical-chemistry methods were employed to measure the energy content of prespawning eulachon. The total energy value of eulachon in Berners Bay was calculated by multiplying eulachon-abundance estimates determined from the acoustic surveys by the measurements of eulachon energy content. Prespawning eulachon were collected 27–28 March 2002 outside Berners Bay in Lynn Canal and 23 and 29 April 2002 and 8 April 2003 in Berners Bay. The samples were pooled to increase sample size and because the energy values for the 2 years were not significantly different (two-sample t test, P = 0.17, df = 7). To ensure sample integrity, fish were frozen immediately after sampling, which also included recording fork length, total body weight, and sex. Fish were either flash-frozen and stored in liquid nitrogen (–196 °C) or vacuum-sealed, individually frozen, and stored in a –20 °C commercial-grade freezer for up to 10 days. Specimens then were transferred and stored in a –80 °C freezer and were analyzed within 3 months.

Energy content of individual fish was calculated as the sum of the calories contributed by the total-body lipid and protein fractions, using the commonly accepted conversion factors of 9.50 kcal·g^{-1} for lipid and 5.65 kcal·g^{-1} for protein (Watt and Merrill 1963). Energy contents determined directly through bomb calorimetry and indirectly through calculation of body composition are found to be similar when the correct conversion factors are used (Craig et al. 1978). Payne et al. (1999) used the same factors for northeast Pacific forage fish species. Carbohydrates are considered negligible in fish and were not included in calculations (Watt and Merrill 1963; Stansby 1976; Montevecchi and Piatt 1984). Individual fish were homogenized while frozen and aliquots of the total-body fish homogenate were randomly selected for the analyses. A 0.5- to 1.0-g aliquot of homogenate was used for lipid analysis. Lipid was extracted using a solution of 2:1 v:v chloroform:methanol in an accelerated solvent extractor with two cycles on a temperature/pressure regime of 120 °C and 8.27 million Pa. The resultant filtrate was washed twice with a 0.5% KCl solution and 1:1 v:v methanol : deionized water to remove the coextractables. Percent lipid was calculated gravimetrically.

Moisture content was determined gravimetrically by drying ~4 g of the sample homogenate in a 75 °C drying oven until a constant weight was achieved. After percent moisture was calculated, samples were ground to a fine powder and nitrogen content was analyzed using a nitrogen analyzer. Percent protein was calculated from the nitrogen content using a conversion factor of 6.25 (Craig et al. 1978). Total-body lipid and protein contents were converted from relative percentages to masses on a wet-weight basis and then multiplied by their corresponding conversion factors to calculate total-body energy content.

Results

Eulachon abundance

Eulachon abundance in Berners Bay increased during early April, was high during mid-April, and then decreased in both study years (Table 1, Fig. 2). Eulachon were much more abundant in 2002 than in 2003. Eulachon abundance peaked at 139 t in 2002 and 30 t in 2003. The period of greatest eulachon abundance was at least 7–10 days each year. The period of greatest abundance was at least 7 days in 2002 (≥40% of peak abundance from 17 to 23 April 2002) and at least 10 days in 2003 (≥40% of peak abundance from 8 to 17 April 2003). Eulachon disappeared from Berners Bay by 6 May in 2002 and by 29 April in 2003. Eulachon were shallower in 2002 than in 2003. Eulachon were most abundant (~90% of biomass) from 40 to 150 m depth in 2002 and from 60 to 150 m in 2003.

Eulachon prespawning aggregations moved from Point Saint Mary to Slate Creek Cove to Berners River Gully and then

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Table 1. Eulachon (*Thaleichthys pacificus*) abundance (t) by area of Berners Bay, Alaska, during April and May 2002 and April 2003.

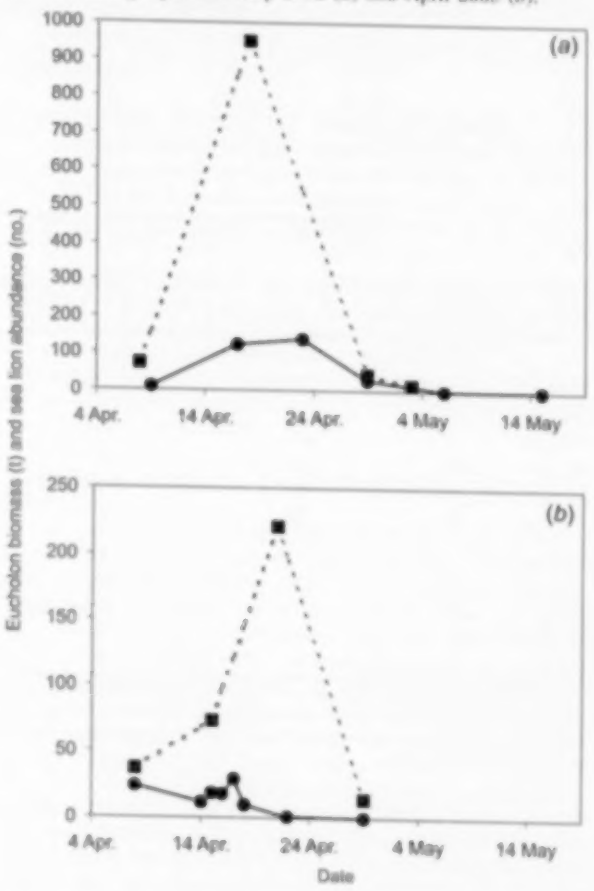
Date	Point Saint Mary to Cove Point	Slate Creek Cove	Berners River Gully	Total
2002				
9 Apr.	10	0	0	10
17 Apr.	80	35	9	124
23 Apr.	2	87	50	139
29 Apr.	0	0	27	27
6 May	0	0	0	0
15 May	0	0	0	0
2003				
8 Apr.	24	0	0	24
14 Apr.	11	0	0	11
15 Apr.	19	0	0	19
16 Apr.	2	16	0	18
17 Apr.	14	16	0	30
18 Apr.	0	10	0	10
22 Apr.	0	1	0	1
29 Apr.	0	0	0	0

to the Berners River system. The aggregations first appeared in Berners Bay near Point Saint Mary and subsequently appeared in Slate Creek Cove (Table 1). The aggregations were last observed in Berners River Gully in 2002 but not in 2003. However, eulachon entered the Berners River system on 19 April 2003 and must have passed through Berners River Gully to reach the rivers. The eulachon prespawning aggregations may form in Berners Bay. No eulachon aggregations were detected during acoustic surveys of Lynn Canal south of Berners Bay on 19 March 2002 and 10 March 2003. We observed sea lions cooperatively foraging inside, but not outside, Berners Bay.

The timing of the eulachon pulse appears more or less predictable. Preliminary fieldwork was conducted from 6 April to 4 May 2001, however, with a simpler echo sounder than was used during 2002; eulachon school volumes could be inferred, but not biomass. Eulachon abundance was greatest on 18–20 April 2001, 17–23 April 2002, and 8–17 April 2003. Eulachon began their spawning runs into the Berners River system between 3 and 6 May during 1995–1997 (Marston et al. 2002), before 27 April 1998 (personal communication, M. Willson, School of Fisheries and Ocean Sciences, University of Alaska, Juneau, AK 99801, USA), on 22 April 2002, and on 19 April 2003 (personal communication, R. Spangler, US Forest Service, Girdwood, AK 99587-0129, USA). Steller sea lions were first observed foraging cooperatively on 6 April 2001, 8 April 2002, and 15 April 2003.

The estimates of eulachon abundance are highly variable. The coefficient of variation from replicate surveys ranged from 29% to 64% (Table 2). For example, the 95% confidence interval for 16 April 2003 ranged from 0 to 122 t (Table 2). The confidence intervals are wide because eulachon are aggregated and the size and density of each aggregation are variable. For example, eulachon were observed on only 9% of the survey transects during 8–17 April 2003, the period of greatest eulachon abundance in 2003, and the coefficient of variation for these transects averaged 67%. Further survey replication helps improve variance estimates. Eight surveys were completed during 14–18 April 2003. Treating the eight surveys as replicate surveys, average abundance for the week is 18 t and the 95% confidence interval ranged from 10 to 26 t. Clearly, variance estimates are greatly improved if time is available to conduct replicate surveys.

Fig. 2. Eulachon (*Thaleichthys pacificus*) biomass (●) and sea lion (*Eumetopias jubatus*) abundance (■) in Berners Bay, Alaska, during April and May 2002 (*a*) and April 2003 (*b*).



Steller sea lion abundance

Berners Bay

In both years, Steller sea lions were first detected inside Berners Bay on 8 April near Point Saint Mary and later became more concentrated around Slate Creek Cove and the Berners River Gully. Sea lions were not observed in the water outside Berners Bay in late March of 2002 or 2003 during aerial surveys of Lynn Canal. During 2002, the peak count of 949 sea lions occurred on 18 April (Table 3, Fig. 2) and was composed of five different groups of sea lions aggregated in the water around the Berners River Gully (group sizes were 62, 53, 174, 263, and 397). The largest group of

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Table 2. Eulachon abundance, lower and upper 95% confidence intervals, and coefficient of variation (CV) based on replicate surveys of Berners Bay, Alaska, in 2003.

	Biomass (t)			95% confidence interval		
Date	Survey 1	Survey 2	Avg.	Lower	Upper	CV (%)
14 Apr.	11					
15 Apr.	19					
16 Apr.	26	10	18	0	122	64
17 Apr.	36	24	30	0	106	29
18 Apr.	12	8	10	0	35	30
14–18 Apr.			18	10	26	54

Note: Replicate surveys were conducted during 14–18 April 2003.

Table 3. Numbers of Steller sea lions (*Eumetopias jubatus*) counted during aerial surveys in water at Berners Bay and at sea lion haulouts (Benjamin Island, Met Point, Gran Point) in Lynn Canal during April and May 2002 and April 2003.

Date	Berners Bay (in water)	Benjamin Island (haulout)	Met Point (haulout)	Gran Point (haulout)	Total no. at haulouts	Grand total	Percentage of southeast Alaska population
2002							
8 Apr.	72	481	14	470	965	1037	4.7
18 Apr.	949	335	37	872	1244	2193	10.0
29 Apr.	45	82	178	1087	1347	1392	6.3
3 May	16	29	ns	ns	29	45	<0.1
2003							
8 Apr.	37	422	ns	ns	422	459	2.1
15 Apr.	73	217	36	543	796	869	4.0
21 Apr.	221	104	4	878	986	1207	5.5
29 Apr.	14	50	0	1145	1195	1209	5.5

Note: The population estimate of 21 933 for the southeast Alaska sea lion population is based on the total of 4874 pups counted during summer of 2002 (National Marine Fisheries Service, Alaska Fisheries Science Center, National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115-0070, USA, unpublished data) multiplied by 4.5 (Calkins and Pitcher 1982). A regionwide Steller sea lion survey was conducted in 2002 but not in 2003; ns, no survey was conducted.

sea lions was synchronously diving and surfacing repeatedly. During these group foraging events, sea lions dive and travel synchronously, with submergence lasting about 1 min between brief intervals of surface travel. The other four groups of sea lions were resting at the surface in large rafts. Sea lions also were counted from the acoustic vessel on 23 April because no aerial survey was conducted that week; the count was 301 animals. On 29 April, 45 sea lions were observed in the bay, and on 15 May, only one was observed.

The temporal distributions of sea lions were similar in 2003, with 37 sea lions observed on 8 April 2003 and the number of sea lions decreasing in late April once eulachon entered the rivers to spawn. However, the peak count of 221 sea lions on 21 April 2003 was substantially lower than the peak count of 949 sea lions on 18 April 2003.

The spatial distribution of sea lions was similar in both years, with sea lions first appearing near the western terminus of the bay near Point Saint Mary and later moving along the shoreline towards the mouths of the Berners/Lace and Antler rivers. Some sea lions entered the Berners River system following the peak of sea lion and eulachon abundance in Berners Bay during 2002. Steller sea lion abundance in the Antler River began rapidly increasing on 28 April, peaking at 120 animals on 30 April, before dropping to near zero on 2 May (personal communication, R. Spangler, US Forest Service, Girdwood, AK 99587-0129, USA). Other sea lions left the Berners Bay area altogether. On 29 April, several small groups of sea lions were seen traveling north along the shoreline outside of the bay, possibly en route to later eulachon spawning runs north of Berners Bay (J. Womble, unpublished data).

Lynn Canal sea lion haulout sites

Benjamin Island is located 22 km from Berners Bay and is occupied seasonally, primarily from October to May. Sea lion abundance decreased at Benjamin Island, the closest haulout to Berners Bay, as sea lion numbers increased in Berners Bay in 2002 and 2003 (Table 3). Abundance at Benjamin Island began decreasing in late March and continued decreasing through April and May. Two other haulouts, Gran Point and Met Point, lie within 60 km of Berners Bay and likely contributed to the peak count of sea lions observed at Berners Bay. Adult female sea lions with dependent pups likely return to these haulout sites in Lynn Canal to provision their pups between foraging bouts to Berners Bay. During the eulachon prespawning aggregation in Berners Bay, most sea lions observed at Berners Bay were either adults or juveniles, whereas most sea lions observed at Benjamin Island were 10- to 11-month-old pups (J. Womble, unpublished data), many of which were likely still dependent upon their mothers for nutrition. Numbers of sea lions increased at Met Point and Gran Point after the number of sea lions peaked in Berners Bay, with a peak of about 1100 sea lions at Gran Point on April 29 both years, and this may

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Table 4. Energy content (mean ± standard error, $n = 22$) of prespawning eulachon expressed in kilojoules relative to total body wet and dry mass.

Wet mass (kJ·g^{-1})	Dry mass (kJ·g^{-1})	Whole body (kJ)
9.70±0.24	32.19±0.59	375.80±35.90

Note: Energy content was calculated using the following coefficients: 9.50 kcal·g^{-1} for lipid and 5.65 kcal·g^{-1} for protein (Watt and Merrill 1963); 1 cal = 4.1868 J. Samples were collected in or near Berners Bay, Alaska, during April and May 2002 and April 2003.

have been a response to eulachon, herring, and capelin spawning aggregations that occur later in northern Lynn Canal.

Eulachon energy content

Eulachon energy density was 9.70 ± 0.24 kJ·g^{-1} wet mass (Table 4). The energy content of an individual fish was 375.8 ± 35.9 kJ, mean length being 179 ± 6 mm and mean weight 39.3 ± 3.9 g. Eulachon energy density was multiplied by the eulachon biomass estimates to obtain estimates of the total energy content of the eulachon in Berners Bay. Eulachon energy content peaked at 1.4 billion kJ in 2002 and 0.29 billion kJ in 2003 (Table 5).

Importance of eulachon for Steller sea lions' energy needs

We inferred the importance of eulachon for Steller sea lions' energy needs by comparing the total energy contributed by the eulachon prespawning aggregation (Table 5) with an estimate of Steller sea lions' daily energy ration. Winship et al. (2002) estimated the total food requirements of Steller sea lions in Alaska. Dividing their estimate of total food requirement by the population size cited in their paper provides an estimate of daily food ration (Table 6). We converted the estimate of daily food ration (15.6 kg·day^{-1}) to daily energy ration using the diet composition and prey energy density values in Winship et al. (2002) (Table 6). The computed value of daily ration was 79 464 kJ·day^{-1} per individual. The maximum value of eulachon energy content in 2002 was 1.4 billion kJ, equivalent to 17 000 daily energy rations (Table 5), far more prey than needed by the maximum number of sea lions (949) observed (Table 3). Although eulachon abundance was less in 2003, the maximum number of daily energy rations was 3600, again far more prey than needed by the maximum number of sea lions (221) observed. A large surplus of prey was available in Berners Bay for the attending sea lions, not only at peak eulachon and sea lion abundance, but also throughout the 3-week period in 2002 from 9 to 29 April and in 2003 from 8 April until the eulachon entered the Berners River system on 19 April. During these two periods of eulachon availability, roughly 15 times more food in 2002 and roughly 10 times more in 2003 was present in Berners Bay than the sea lions' daily requirement.

The computed value of daily ration is an average value for Alaska (Table 6). We used an average estimate of energy requirements because we do not have detailed age and sex information for the sea lions in Berners Bay. We tested the sensitivity of this estimate to different age and sex compositions. A pregnant, lactating female late in gestation requires the most energy among all sexes and ages, about 200 000 kJ·day^{-1} (Winship et al. 2002). This value is 2½ times the average value. Therefore, even if all sea lions in Berners Bay were this life stage, more than enough food was available for all sea lions present during the two periods of eulachon availability (9–29 April 2002 and 8–18 April 2003).

Discussion

Steller sea lion foraging and eulachon availability

Foraging by Steller sea lions was associated with the presence of a prespawning aggregation of eulachon in Berners Bay. Steller sea lion abundance increased as eulachon began concentrating in Berners Bay, peaked as eulachon abundance peaked, and decreased as the eulachon moved up-river. As sea lion abundance increased in Berners Bay, the number of sea lions decreased at Benjamin Island. In contrast, the number of sea lions at Met Point and Gran Point increased after the peak number of sea lions occurred in Berners Bay. Several times, Steller sea lions were observed diving and presumably foraging in locations where eulachon aggregations were observed acoustically.

Importance of eulachon for Steller sea lions' energy needs

The eulachon prespawning aggregation provided an abundant, albeit temporary, prey for Steller sea lions. A large surplus of prey was available per sea lion while the eulachon aggregation was present, so that all of the sea lions in Berners Bay could have fed to satiation on prey that were relatively easy to catch, energy-rich, and spatiotemporally predictable on an annual basis. This computation of energy rations assumes the average energy density of diet (5.09 kJ·g^{-1}) and average daily food ration (15.6 kg·day^{-1}) reported by Winship et al. (2002). Eulachon energy density (9.70 kJ·g^{-1}) is higher than the average, therefore a sea lion may increase its energy intake by 91% during the time eulachon are aggregated in Berners Bay while eating the same quantity of food. This computation of increased energy intake considers average, not maximum, food intake, as in Marston et al. (2002). Energy intake may be higher than average, owing to concentration of eulachon and thus increased availability.

Up to 949 Steller sea lions were present in Berners Bay during 2002; however, it is likely that sea lions at haulouts in Lynn Canal also were traveling to Berners Bay to forage on eulachon. If the total number of sea lions at haulouts in Lynn Canal is included, 10% of the estimated number of sea lions in southeast Alaska were found in Berners Bay and at haulouts in Lynn Canal during the peak of eulachon abundance in Berners Bay. The population estimate of 21 933 is based on a total count of 4874 pups in southeast Alaska during the summer of 2002 (National Marine Fisheries Service, National Marine Mammal Laboratory, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115-0070, USA, unpublished data) multiplied by 4.5 times the number of pups counted (Calkins and Pitcher 1982).

Thirty-three eulachon spawning runs have been documented for southeast Alaska including Berners Bay. Although eulachon abundance has been estimated only at Berners Bay, we know that other eulachon spawning sites in southeast Alaska attract seasonal aggregations of Steller sea lions. For example, during late winter and early spring of 2000–2003, large numbers of sea lions (at least 800 each year) were hauled

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Table 5. Date, biomass, number, and energy content of eulachon, and number of daily energy rations due to eulachon available for Steller sea lions in Berners Bay, Alaska, during April and May 2002 and April 2003.

Date	Biomass (t)	Number (millions)	Energy content (billions kJ)	No. of daily energy rations (thousands)
2002				
9 Apr.	10	0.22	0.10	1.2
17 Apr.	124	2.76	1.21	15.2
23 Apr.	139	3.10	1.35	17.0
29 Apr.	27	0.60	0.26	3.3
6 May	0	0.00	0.00	0.0
15 May	0	0.00	0.00	0.0
2003				
8 Apr.	24	0.46	0.23	2.9
14 Apr.	11	0.21	0.11	1.4
15 Apr.	19	0.35	0.18	2.3
16 Apr.	18	0.34	0.17	2.2
17 Apr.	30	0.56	0.29	3.6
18 Apr.	10	0.18	0.09	1.2
22 Apr.	1	0.01	0.01	0.1
29 Apr.	0	0.00	0.00	0.0

Table 6. Prey category, mean annual biomass consumption, energy density, and mean annual energy consumption for Steller sea lions in Alaska.

Prey category	Mean annual biomass consumption (thousands t)	Energy density ($kJ \cdot g^{-1}$)	Mean annual energy consumption (billions kJ)
Cephalopods	14.6	5	73
Flatfish	13.1	4	52
Forage fish	40.5	7.5	304
Gadids	144	4	576
Hexagrammids	97.5	4.5	439
Other	30.9	4.5	139
Salmon	78.7	7	551
Total	419.3		2134

Note: Biomass consumption and energy-density values are from Winship et al. (2002). Daily energy ration is 79 464 kJ, based on the energy-consumption value and the size of the sea lion population in Alaska in 1998, which was 73 570 individuals (Winship et al. 2002). Daily food ration is 15.6 kg, based on the mean annual biomass consumption and size of the sea lion population.

out at Dry Bay, near the mouth of the Alsek River. The timing coincides with the eulachon spawning run in the Alsek River (personal communication, W. Lucey, US Forest Service, Yakutat, AK 99869, USA). During spring 2002, aerial surveys were conducted at 18 eulachon spawning sites in southeast Alaska to document the numerical response of sea lions. Large aggregations of sea lions in excess of 200 animals were documented at Berners Bay, Taku Inlet, Lutak Inlet, and Taiya Inlet (Womble 2003).

Characteristics of the eulachon pulse

Several characteristics of the eulachon pulse in Berners Bay make it attractive for Steller sea lions. The timing of the eulachon pulse is more or less predictable. The period of greatest eulachon abundance, the beginning of the spawning run, and the first observation of Steller sea lions cooperatively foraging all occurred within a narrow window of dates only 10–17 days long. For example, the period of greatest eulachon abundance always occurred sometime between 8 and 23 April during 2001–2003. The location of the eulachon prespawning aggregation appears predictable. Eulachon were found in the western and northern parts of Berners Bay from 2001 to 2003, as were foraging Steller sea lions. Steller sea lion foraging may be facilitated by spatial features in Berners Bay. Eulachon in the western part of Berners Bay are constrained by the western shore. Cooperative foraging by Steller sea lions has been observed there many times during several years. The western shore may facilitate foraging by providing a physical boundary on one side of the group of foraging sea lions. Eulachon in the northern part are constrained by the limits of the submarine gully. The gully walls may facilitate foraging by limiting eulachon escape.

The eulachon spawning aggregation is a target for predators because eulachon are densely aggregated and high in energy content. Eulachon energy density ($9.70\ kJ \cdot g^{-1}$ wet mass) is much higher than that of other forage fish species in the Gulf of Alaska (capelin, *Mallotus villosus*, 5.04; Pacific

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herring, *Clupea pallasii*, 5.84; Pacific sand lance, *Ammodytes hexapterus*, 5.74) except northern lampfish, *Stenobrachius leucopsarus* (8.50) (Anthony et al. 2000). Both northern lampfish and eulachon are energy-rich, but prespawning eulachon likely are easier targets because they occur mainly in aggregations between 40 and 150 m depth. In contrast, northern lampfish in Lynn Canal in March 2002 were distributed in a diffuse layer below 200 m. Eulachon also are an attractive energy source when in-river, because the energetic benefit/cost ratio is likely high for the relatively weak-swimming eulachon, which are generally concentrated in the low-velocity shallow waters at river margins (Marston et al. 2002).

Other predators besides Steller sea lions use predictable prey. Piscivorous seabirds in the Skagerak–Kattegat region (northeast Atlantic Ocean) were correlated with relatively stable and predictable aggregations of herring (*Clupea harengus*) but not with abundant, less stable sprat (*Sprattus sprattus*), suggesting the tendency for seabirds to depend on predictable concentrations of prey (Skov et al. 2000). Killer whales (*Orcinus orca*) in northern Norway were encountered most frequently during October–January, when spring-spawning herring wintered (Similä et al. 1996).

Importance of the eulachon prespawning aggregation for Steller sea lions

Steller sea lions face increased energetic demands during spring before the breeding season (Winship et al. 2002), thus the availability of eulachon during spring may be critical for both males and females. For females, the later stages of gestation occur during spring and likely increase energetic demands. The energy cost of early gestation is minimal, but most fetal mass in mammals accrues during the third trimester (Frazer and Hugget 1974). In addition to carrying a developing fetus, most (61%) adult females are still lactating in May (Calkins and Pitcher 1982), so they are foraging to meet not only their own energy demands but also those of a nursing pup. Lactation is one of the most energetically demanding activities for mammals (Gittleman and Thompson 1988). Bioenergetic modeling implies that a female Steller sea lion nursing a dependent pup requires 70% more food than a female without a pup (Winship et al. 2002). After parturition, females may fast for up to 11–14 days before leaving the rookery on a foraging trip (Gentry 1970; Sandegreen 1970). Thus, female Steller sea lions face high-energy demands during April and May while in the third trimester of gestation and simultaneously nursing a pup. Building up fat stores prior to parturition likely is important to sustain both mother and pup during the post-parturition fasting period.

Adult male sea lions may fast for up to 68 days (Gentry 1970; Sandegreen 1970; Gisiner 1985) to allow them to acquire and maintain a territory at the rookery during the breeding season. Building energy stores prior to the breeding season likely affects their reproductive success by determining their ability to acquire and hold a territory and the number of females they mate with. Thus, both sexes have high energy requirements during spring and their reproductive success likely is influenced by access to spawning runs of high-energy, densely aggregated prey. The relationship between the availability of energy-rich prey and the timing of reproduction has been observed for other mammals, such as the mink (*Mustela vison*), whose lacation period coincided with the availability of carcasses of Pacific salmon (*Oncorhyncus* spp.) (Ben-David 1997).

The response of Steller sea lions to prespawning aggregations of eulachon in Berners Bay demonstrates the importance of seasonally available energy-rich prey, which occurs at an energetically demanding time for sea lions. Because the availability of eulachon is ephemeral, the presence of eulachon in the diet of sea lions may be difficult to detect unless diet studies are conducted more frequently. Although this study does not directly address the "nutritional-stress hypothesis" (Trites and Donnelly 2003), our results imply that prey species available for brief time periods may impact trends in Steller sea lion abundance. Our study provides evidence that the availability of some prey species shows extreme temporal variation and that the period of availability coincides with an energetically demanding period for consumers. Another seasonally aggregating species besides eulachon that is likely important for marine predators in southeast Alaska is Pacific herring. Based on observations of Steller sea lions in southeast Alaska, the availability of seasonally abundant energy-rich prey could be a significant factor for the reproductive success and survival of Steller sea lions throughout their range. More research is required to document sea lion prey availability at critical times and, in general, further study of the relationships between seasonally important prey species and their predators in the northeastern Pacific Ocean is needed.

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Changes in the $\delta^{13}C$ of pelagic food webs: the influence of lake area and trophic status on the isotopic signature of whitefish (*Coregonus lavaretus*)

Marie-Elodie Perga and Daniel Gerdeaux

Abstract: We investigated the relationships between the pattern of variation of $\delta^{13}C$ in pelagic food webs and various morphologic and trophic characteristics of peri-alpine lakes. We used the $\delta^{13}C$ of whitefish (*Coregonus lavaretus*), a long-lived zooplanktivorous fish, to assess the isotope ratio of dissolved inorganic carbon (DIC) at the origin of the pelagic food web. The $\delta^{13}C$ of DIC depends on its origin, which may be the atmosphere or the mineralization of organic matter. A synchronic study of 22 peri-alpine lakes shows that the surface area of the lake accounts for much of the variability of the $\delta^{13}C$ in pelagic food webs ($r^2 = 0.76$). The $\delta^{13}C$ increases with lake size, which suggests that the origin of the DIC integrated into the pelagic food web depends on lake size. To differentiate the influence of trophic status from morphological effects, a diachronic study was performed on the $\delta^{13}C$ of fish scales collected over the 20-year re-oligotrophication of Lake Geneva. The $\delta^{13}C$ of whitefish increased with phosphorus concentration ($r^2 = 0.71$). This pattern is related to the growing demand for atmospheric DIC as primary production increases.

Résumé : Nous avons étudié le profil de variation du $\delta^{13}C$ des réseaux trophiques pélagiques en fonction de différentes caractéristiques morphologiques et trophiques de lacs péri-alpins. Nous avons utilisé la signature isotopique du corégone, *Coregonus lavaretus*, un poisson zooplanctonophage à longue durée de vie, pour obtenir une estimation de la signature du carbone inorganique dissous (CID) à l'origine du réseau trophique pélagique. Le $\delta^{13}C$ du CID dépend de son origine : atmosphérique ou issu des processus de minéralisation de la matière organique. Par une étude synchrone sur 22 lacs péri-alpins, nous avons montré que la surface est le facteur qui explique la plus grande part de la variabilité du $\delta^{13}C$ ($r^2 = 0.76$). La signature $\delta^{13}C$ du corégone augmente avec la taille du lac, indiquant que l'origine du CID intégré dans le réseau pélagique dépend de la taille du système. Pour étudier l'influence du statut trophique en se dégageant de l'influence de la taille du lac, nous avons mené une étude diachronique, à partir d'une collection d'écailles couvrant la période de re-oligotrophisation du lac de Genève (20 ans). Le $\delta^{13}C$ du corégone augmente avec la concentration en phosphore ($r^2 = 0.71$), en relation avec un besoin croissant en CID d'origine atmosphérique lorsque la production primaire augmente.

Introduction

Stable-isotope analysis has been used with great success over the past 20 years because it is very useful for studying food webs and energy flows in both terrestrial and aquatic ecosystems, especially in lakes (Yoshioka et al. 1994; Zohary et al. 1994; Grey et al. 2001). Many studies have been conducted on food webs in individual lakes throughout the world, yielding measurements of the two main isotope ratios used in stable-isotope analysis. The ratio of stable isotopes of nitrogen ($\delta^{15}N$) in the consumer is typically enriched by 3‰–4‰ relative to the diet and can be used to estimate trophic positions (De Niro and Epstein 1981; Minagawa and Wada 1984). In contrast, the ratio of stable isotopes of carbon ($\delta^{13}C$) is transmitted with little change from the diet to the consumer (De Niro and Epstein 1978), which makes it helpful for tracking the ultimate sources of the carbon in an organism, provided the isotopic signatures of the sources are different (France 1995, 1996*b*). Cross-system examination of these isotopic data reveals high between-lake differences in the isotopic signatures of food webs (Gu et al. 1996; France et al. 1997; France 2000). In pelagic food webs, for example, $\delta^{13}C$ ranges from –20‰ (Quay et al. 1986) to –50‰ (Rau 1978).

The $\delta^{13}C$ of organisms reflects the $\delta^{13}C$ of the carbon at the base of the food web (Fry and Sherr 1984; Peterson and Fry 1987), and this depends on the $\delta^{13}C$ of the primary carbon sources (e.g., phytoplankton, benthic or littoral attached algae, detritus) and the proportions in which they are exploited by the pelagic food web (Grey et al. 2000). Moreover, the $\delta^{13}C$ of the primary producers is imposed by the origin of the inorganic carbon used (atmosphere, dissolution

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Table 1. Morphological and trophic data and mean whitefish isotopic signatures from the set of peri-alpine lakes studied.

Lake	Country	Max. depth (m)	Mean depth (m)	Max. length (km)	Max. width (km)	Shoreline length (km)	Area (km^2)	Vol. (km^3)	Residence time (year)
Quatre Cantons	Switzerland	214	104	1	3.6	144.0	114	11.80	1.0
Aiguebelette	France	71	30	4	3.0	14.2	5.5	1.60	2.9
Annecy	France	65	41	15	3.2	32.0	27.6	1.10	3.8
Bienne	Switzerland	74	30	15	4.1	50.0	39.3	1.20	0.2
Bourget	France	145	81	18	3.0	44.8	42.0	3.60	3.8
Brienz	Switzerland	261	173	14	2.8	36.0	29.8	5.20	2.7
Chalain	France	32	16	3	1.1	7.5	2.3	0.04	0.9
Constance	Switzerland and Germany	254	100	63	14.8	160.0	476.0	47.70	4.3
Ilay	France	32	11	2	0.4	5.0	0.7	0.01	1.0
Joux	Switzerland	32	15	9	1.2	24.0	8.7	0.13	3.2
Geneva	Switzerland and France	309	152	72	13.5	200.2	582.0	89.0	11.4
Maggiore	Italy	372	178	66	10.1	140.0	212.5	37.50	4.1
Neuchâtel	Switzerland	152	64	38	8.1	95.0	217.9	13.98	8.2
Rousses	France	18	8	2	0.5	4.1	0.9	0.01	1.0
Sarnen	Switzerland	52	32	17	3.6	15.3	7.6	0.24	0.7
Starnberg	Switzerland	128	53	7	1.1	49.2	56.4	3.00	21.0
St Point	France	41	19	20	2.8	14.2	4.2	0.08	0.5
Sylans	France	20	10	2	0.2	3.9	0.5	0.01	3.8
Thune	Switzerland	217	135	17	3.5	50.0	48.4	17.50	1.9
Vouglans	France	100	38	30	0.8	78.0	16.0	0.60	0.5
Walenstadt	Switzerland	145	103	21	2.9	34.1	24.1	2.52	1.5
Zurich	Switzerland	48	23	39	3.9	30.1	20.3	0.47	0.2

Note: NA, not available; Max., maximal; Vol., volume; concn., concentration; Min., minimal.
[a]Minimal O_2 concentration at the bottom.

of carbonates, and (or) respiration) and by inorganic carbon limitation (Raven et al. 1994; France 1996*a*).

The $\delta^{13}C$ therefore encapsulates a lot of information about the carbon-supply processes in the food web. By studying the pattern of variation of pelagic $\delta^{13}C$ in lakes, we hope to tease out the lake factors that exert a major influence on carbon sources in pelagic food webs.

We could have used zooplankton (France et al. 1997), sediment, or plankton (Gu et al. 1996) to estimate the $\delta^{13}C$ of the organic matter exploited by the pelagic food web. However, the isotopic signatures of short-lived organisms are subject to strong temporal variability (Yoshioka et al. 1994; Zohary et al. 1994). Moreover, zooplankton makes vertical migrations but is not very mobile on the horizontal plane, and is also subject to marked spatial variability. To get round these problems, we used a spatial and temporal integrator (Post 2002) of pelagic signatures: a long-lived zooplanktivorous fish, the whitefish (*Coregonus lavaretus*). Fish dorsal muscle reflects dietary $\delta^{13}C$, with nearly no fractionation (De Niro and Epstein 1978). Scales are, on average, 4‰ enriched in ^{13}C compared with muscle (SD = 1.26‰) and can be used as a 4‰ translated proxy of food $\delta^{13}C$ (Perga and Gerdeaux 2003). As these are low-turnover tissues, the variability of the $\delta^{13}C$ of the pelagic food web is integrated over the year by the muscle and over the life-span by the scales (Tieszen et al. 1983).

The pattern of variation of $\delta^{13}C$ was studied in two different ways. The first was a synchronic approach, in which relationships between the $\delta^{13}C$ of the pelagic food web and some morphological and trophic variables were identified in a set of 22 alpine lakes. A diachronic study was then performed on the $\delta^{13}C$ of a collection of fish scales covering the 20-year re-oligotrophication of Lake Geneva, to distinguish between the influence of trophic status and morphological effects.

Materials and methods

For the comparative study, whitefish caught with experimental or commercial gear were sampled in 22 lakes located in the peri-alpine part of the Alps in France, Switzerland, Germany, and Italy. To avoid variability due to a potential ontogenic shift, we sampled individuals that were similar in age class. Homogeneity in age was checked by means of scalimetry. A small section of dorsal muscle was taken for isotopic analyses. The lakes ranged in surface area from 0.72 to 582 km^2, and they contained 2–60 $\mu g \cdot L^{-1}$ total phosphorus. The attributes of the lakes are shown in Table 1. For the study centered on Lake Geneva, whitefish scales were obtained from a collection made from spawning fish (1980–2001). Scales from 8–10 mature adults caught in 1980, 1982, 1985, 1988, 1990, 1991, 1993, 1995, 1996, 1997, 1998, and 2001 were decalcified and analyzed (Perga and Gerdeaux 2003). Samples were freeze-dried and finely ground in a ball mill. Samples of muscle (1 mg) and scale (1.5 mg) were weighed in 6 mm × 4 mm tin cups for continuous-flow isotope-ratio mass spectrometry analysis using a Europa Scientific ANCA-NT 20–20 stable-isotope analyzer with a NCA-NT solid/liquid preparation module (PDZ Europa Ltd., Crewe, UK). Analytical precision was 0.2‰, estimated from five standards analyzed along with the samples. The working standards used were 1 mg leucine, prepared by freeze-drying

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Watershed area (km²)	P_{total} (µg P·L⁻¹)	NO_3 concn. (mg·L⁻¹)	Min. O_2 concn. (mg·L⁻¹)*	$\delta^{13}C$ (‰)	*n*
1 831	5	0.57	3.4	–30.5	12
60	25	0.44	0.4	–35.2	11
277	6	0.25	0.5	–32.1	10
8 305	18	1.52	0.5	–29.8	5
560	30	0.71	0.1	–29.8	10
1 127	5	0.39	9.3	–30.9	10
42	20	0.25	0.0	–34.1	20
10 500	14	0.41	6.0	–29.6	20
5	NA	0.11	0.2	–32.8	9
1 994	13	0.54	3.2	–34.3	10
7 393	39	0.56	3.0	–26.5	20
6 386	14	0.81	6.0	–29.2	8
2 670	14	0.54	3.2	–31.8	10
13	10	0.12	4.4	–35.8	9
267	5	0.58	5.5	–31.8	12
314	12	0.54	1.4	–29.8	10
241	50	0.35	3.0	–35.9	8
1 994	NA	1.30	0.0	–38.9	15
2 490	11	0.53	7.6	–31.4	11
1 120	NA	NA	8.1	–34.6	10
1 061	3	0.16	6.1	–31.6	11
1 564	25	0.71	1.1	–33.5	13

50 mL of a 20 mg·mL^{-1} stock solution in the tin cups and calibrated against "Europa flour" and International Atomic Energy Agency standards N1 and N2. All stable-isotope values are reported using the δ notation:

$$\delta^{13}C\ (‰) = [[(^{13}C_{sample}/^{12}C_{sample})/(^{13}C_{standard}/^{12}C_{standard})] - 1] \times 10^3$$

Muscle lipid content varies among individuals, so the $\delta^{13}C$ values were corrected using McConnaughey's formula (McConnaughey and McRoy 1979). The normality of distribution was tested by the Kolmogorov test, and variables were log-transformed to ensure normality when necessary. Relationships between $\delta^{13}C$ and other variables were described by linear regression. A stepwise regression was performed to check whether the model could be improved by adding other explanatory variables. Environmental variables were first screened for correlations, and six explanatory variables that were not strongly correlated were used in a stepwise regression. Mallows' Cp statistics were calculated, and each term was successively added to and dropped from the current model. Statistical analyses were performed using S-PLUS version 6.0 (Insightful Corporation 2001).

Results

Between-lakes comparison

Whitefish $\delta^{13}C$ values ranged from –38.5‰ to –26.5‰ (Table 1). The $\delta^{13}C$ was correlated with all the variables linked to system size (Table 2), the best correlation being obtained for the logarithm of lake surface area ($n = 22$, $r^2 = 0.76$, $p < 10^{-7}$) (Fig. 1). Phosphorus concentration (total phosphorus load, P_{total}) was not significantly correlated with $\delta^{13}C$ in whitefish ($n = 17$, $r^2 = 0.01$, $p = 0.68$; Table 1). The surface area of the lake accounts for 76% of the total variation of $\delta^{13}C$ and, among all variables tested, is the best predictor of the $\delta^{13}C$ isotopic signature of whitefish (Table 1). P_{total} and lake surface area are not correlated ($r^2 = 0.08$, $p = 0.70$).

All the variables relative to system size (e.g., surface area, volume, length) are strongly correlated, whereas chemical variables, residence time, and altitude are more independent. The model is not improved by adding these variables to the regression model (Table 3).

In contrast to previous studies (Gu et al. 1996; France et al. 1997), we found no relationship between whitefish $\delta^{13}C$ and P_{total}. We stratified the lakes by surface area (greater or smaller than the median surface area), and found that $\delta^{13}C$ was positively related to P_{total} for the larger lakes ($r^2 = 0.71$ for area >25.80 km^2; $p = 0.001$, $n = 10$) but not for the smaller ones ($r^2 = 0.44$ for area <25.80 km^2; $p = 0.07$, $n = 7$) (Fig. 2). The absence of a correlation for the smaller lakes is not due to a smaller range of P_{total} values. Mean P_{total} values for the two groups (small lakes, large lakes) were not significantly different (one-way analysis of variance, $F_{[1,17]} = 0.395$, $p = 0.538$).

Lake Geneva

The $\delta^{13}C$ of fish scales decreased from –20‰ to –23‰, and P_{total}decreased from 90 to 30 µg·L^{-1} (Fig. 3*a*). P_{total} and the isotopic signature of the fish scales were significantly and strongly correlated ($r^2 = 0.71$, $p = 0.0005$) (Fig. 3*b*).

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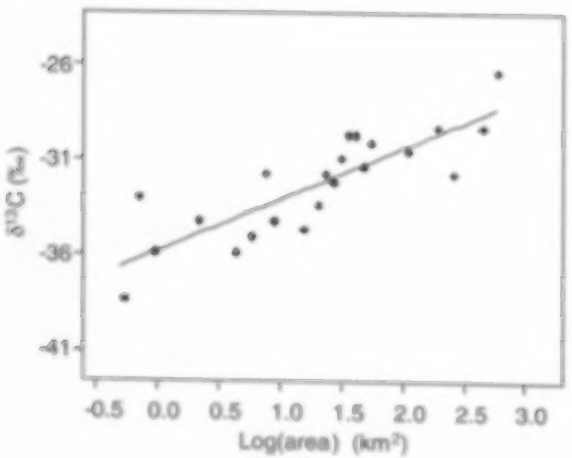
Table 2. Correlations between $\delta^{13}C$ of whitefish and the different variables studied.

Variable	r^2	p
Altitude	0.17	0.052
Maximal depth	0.69	$<10^{-5}$
Mean depth	0.67	0.0009
Shoreline length	0.61	$<10^{-5}$
Maximal length	0.43	0.0009
Maximal width	0.72	$<10^{-5}$
Surface	0.76	$<10^{-5}$
Volume	0.70	$<10^{-5}$
Residence time	0.19	0.040
Watershed area	0.24	0.020
O_2 concentration	0.06	0.243
NO_3 concentration	0.00	0.954
P_{total}	0.01	0.680

Note: All the variables except total phosphorus load (P_{total}) were log-transformed before linear regression.

Fig. 1. Relationship between $\delta^{13}C$ and the logarithm of lake surface area. The regression equation is as follows: $\delta^{13}C = -35.99 + 1.21 \times \log(\text{area})$, $r^2 = 0.766$, $p = 10^{-7}$.



Discussion

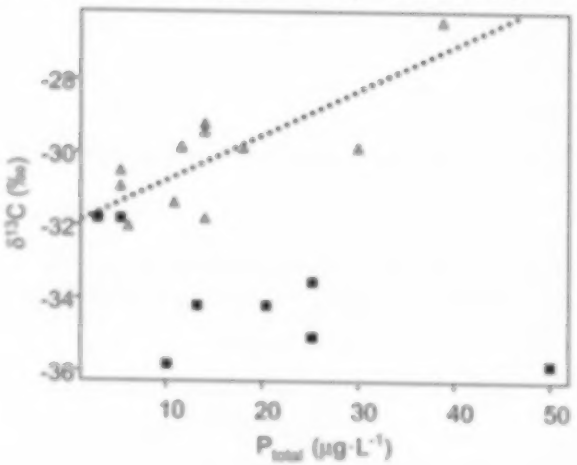
Our findings are based on the assumption that the $\delta^{13}C$, and thus the source of the dissolved inorganic carbon (DIC) integrated into the pelagic food web, can be assessed from the $\delta^{13}C$ of whitefish. The whitefish is usually assumed to be a strictly zooplanktivorous fish, and this is corroborated by all the studies done on whitefish diet in large peri-alpine lakes. In Lakes Constance, Lucerne, Maggiore, and Geneva, whitefish preferentially eat the biggest forms of zooplankton: *Bythotrephes* spp., *Leptodora* spp., *Daphnia* spp., possibly *Bosmina* spp., and copepods (Giussani and De Bernardi 1977; Becker and Eckmann 1992; Mookerji et al. 1998). Yet in smaller lakes, whitefish are occasionally benthic consumers. In several Nordic studies, some ecotypes ate benthic prey, but zooplankton clearly remained their main food (Heikinheimo et al. 2000). The lakes where whitefish ate

Table 3. Results of stepwise multiple regression analysis of the relationships between whitefish $\delta^{13}C$ and environmental variables.

Variable added	Sum of squares	Residual sum of squares	Cp
None		331.78	427.24
P_{total}	0.40	331.38	474.57
NO_3 concentration	2.25	329.53	472.72
Altitude	1.21	330.57	473.75
Residence time	27.34	304.44	447.63
O_2 concentration	0.42	331.35	474.55

Note: The current model is the single regression between $\delta^{13}C$ and log(area). The first line ("none") gives the parameters for the current model. The best model is the one that reduced Cp the most. Adding any of the other variables leads to a higher Cp. The current model is not improved by adding another explanatory variable.

Fig. 2. Relationships between $\delta^{13}C$ and total phosphorus load (P_{total}) for small lakes (■; area <25.8 km^2, $r^2 = 0.4425$, $p = 0.072$, $n = 7$) and large lakes (△; area >25.8 km^2, regression equation: $\delta^{13}C = -31.93 + 0.12 \times P_{total}$, $r^2 = 0.71$, $p = 0.001$, $n = 10$).



chironomids were often less than 20 m deep, even if they covered a large surface area. In fact, the fish fed opportunistically on the most abundant food source, but preferred crustacean zooplankton (Enz et al. 2001; Gerdeaux et al. 2002). During winter and early spring, consumption of chironomid nymphae has been observed in Lake Annecy (Gerdeaux et al. 2002). However, the fish do not grow during this season (Wilson and Pitcher 1984; Fechhelm et al. 1992; Rudstam et al. 1994). We can therefore assume that the isotopic signal of this food is not integrated into the muscle. In contrast, whitefish do consume pelagic zooplankton during the period of somatic growth, when we can assume that the isotopic signature of the diet is integrated into the tissues.

A second assumption is that the trophic position of whitefish is the same in all the lakes. Depending on the ratio of herbivorous zooplankton (*Daphnia* spp.) to predaceous zooplankton (*Bythotrephes* spp., *Leptodora* spp.), the trophic position of whitefish could actually vary, although not by

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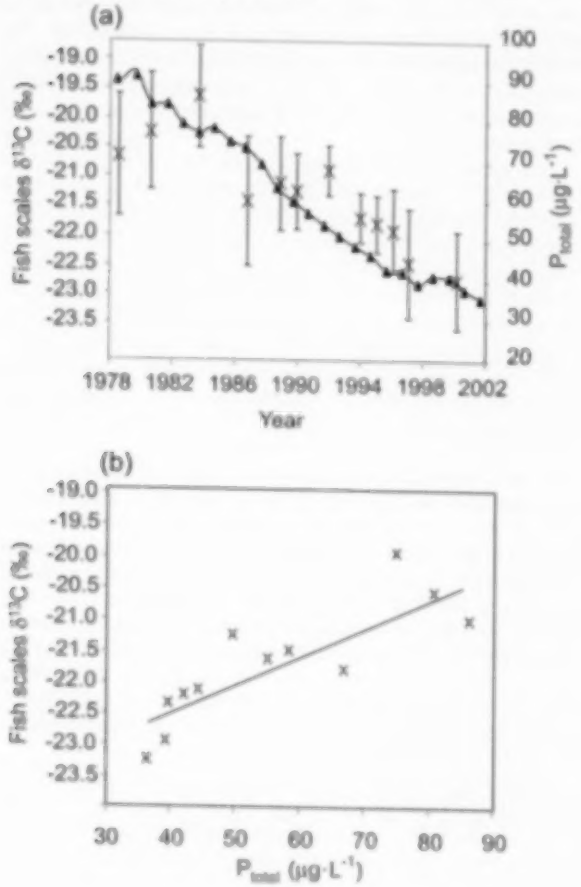
Fig. 3. Relationships between $\delta^{13}C$ and P_{total} during the re-oligotrophication phase in Lake Geneva (1980–2001). (*a*) Evolution of the $\delta^{13}C$ (mean and confidence interval) of fish scales (×) and P_{total} (▲). (*b*) Relationships between mean P_{total} and mean $\delta^{13}C$ of whitefish scales. Regression equation: $\delta^{13}C = -24.30 + 0.046 \times P_{total}$, $r^2 = 0.71$, $p = 0.0005$.



more than one trophic level. The fractionation of $\delta^{13}C$ was settled as inferior to 0.5‰ in aquatic field experiments (Post 2002) and about 0.2‰ in freshwater ecosystems (France and Peters 1997). This means that even if the trophic position of whitefish is not exactly the same in all the lakes, the $\delta^{13}C$ variability introduced will remain negligible. Consequently, whitefish can be used as an integrator of the pelagic-chain $\delta^{13}C$. The $\delta^{13}C$ at the top of the pelagic food web increased with lake size, the most explanatory variable being the surface area. This result is consistent with the relationship established by Post (2002) on the $\delta^{13}C$ of mussels. The correlation between the two variables was closer in our study. Even though the $\delta^{13}C$ of primary producers depends on numerous factors, the variation of $\delta^{13}C$ with lake surface area was attributed to a change in the signature of the DIC pool rather than to a modification of isotope fractionation during photosynthesis (Post 2002). DIC originates from dissolution from the atmosphere, carbonates, or the process of mineralization of organic matter. The DIC derived from dissolution from the atmosphere has a high $\delta^{13}C$, close to 0‰. The photosynthesis process fractionates by preferentially fixing ^{12}C, which leads to $\delta^{13}C$ in the phytoplankton of around –20‰ (Raven et al. 1994). The $\delta^{13}C$ of DIC resulting from mineralization or respiration is comparable to that of the mineralized organic matter, which is already impoverished in ^{13}C (De Niro and Epstein 1978): endogenous DIC has a lower $\delta^{13}C$ than atmospheric DIC, which leaves photosynthetic matter still more impoverished (France et al. 1997; Keough et al. 1998). The high $\delta^{13}C$ in autotrophs illustrates the photosynthetic fixation of atmospheric inorganic carbon, whereas the very low $\delta^{13}C$ of autotrophs is associated with high levels of microbial respiration (France 1999).

Relationships between $\delta^{13}C$ and lake surface area could be attributable to a change in the origin of the inorganic carbon sustaining pelagic primary production. The relative contributions of endogenous and atmospheric inorganic carbon to the pelagic food web may depend on lake size. In smaller lakes, the pelagic food web relies to a significant extent on recycled carbon. In contrast, in larger lakes the ratio of the contributions of atmospheric to endogenous carbon is higher.

The relationships observed between $\delta^{13}C$ and lake surface area could first result from a greater influence of atmosphere in larger lakes. Water bodies with a large surface area are thought to react much more quickly with the atmosphere than small ones because the physics of gas exchange and turbulence regimes are enhanced (Wanninkhof 1992). Then, in larger lakes, endogenous DIC, with low $\delta^{13}C$, could be "diluted" by atmospheric CO_2, enriched in ^{13}C. In that context, the observed pattern could result more from gas exchange between lake and atmosphere than from the specific effect of the food web. However, pCO_2 patterns of variations with lake size have provided evidence that biological effects can also be involved. Kelly et al. (2001) measured lower pCO_2 in large Canadian lakes and higher pCO_2 in small ones. To explain this pattern, Kelly et al. (2001) invoked the physical effects mentioned above. However, as dissolved organic carbon (DOC) concentration was also negatively correlated with lake size in their set of lakes, higher inputs of organic carbon to smaller lakes could also explain the higher pCO_2. DOC measurements were not available for our set of lakes but the importance of exogenous carbon in supporting lake food webs is becoming more and more obvious (Pace et al. 2004).

Post (2002) attributed the relationship between $\delta^{13}C$ and lake size also to the fact that terrestrial inputs are higher in small lakes than in large ones. In the absence of strong anthropogenic pressure, the effects of the watershed on the lake, notably the contribution of allochthonous inputs, can often be assessed from the ratio between the surface areas of the lake and the watershed. Our set of lakes included some highly urbanized ones, and all of them had undergone a phase of eutrophication (Office fédéral de l'environnement des forêts et du paysage (OFEFP) 1994). The values of the lake area – watershed area ratio are not representative of the influence of the watershed on the lake, and do not provide reliable information about the contribution of the terrestrial inputs in our set. This made it impossible to draw any conclusion about the influence of the terrestrial inputs. Yet ben-

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thic and sediment respiration have been shown to make a significant contribution to CO_2 production (Jonsson et al. 2003). The greater stock of respired carbon could also be derived from the mineralization of littoral or benthic inputs to the pelagic zone, which is more important in smaller lakes than in larger ones.

In lakes, the habitat that can be colonized by littoral or benthic algae depends on light attenuation. Consequently, the relative proportions of the littoral or benthic zone and the pelagic zone depend on water transparency and mean depth (Vadeboncoeur et al. 2001). In our set of lakes, mean depth and lake size are strongly correlated. The largest lakes are also the deepest ones. This means that the large lakes have a greater proportion of pelagic zone than smaller ones. The littoral ecotone may therefore have less influence on the pelagic zone in large lakes than in small ones. Littoral and benthic zones are very productive systems, with very effective bacterial mineralization (Vadeboncoeur et al. 2002), and can therefore contribute to the carbon supply of pelagic food webs. Consequently, the relative contribution of benthic or littoral DIC to the pelagic food web may be strongly influenced by lake size in our set of lakes. In small lakes, the contribution of endogenous carbon processing from the mineralization of anthropogenic, terrestrial, benthic, or littoral carbon would make up a larger proportion of the pelagic carbon supply. In large lakes, atmospheric inorganic carbon sustains the pelagic food web.

The strong influence of surface area on $\delta^{13}C$ may mask potential relationships with trophic status. When the lakes were divided into two groups, around the median surface area, two relationships were found. The positive relationship between $\delta^{13}C$ and P_{total} for the large lakes in the synchronic study is consistent with the results of previous studies, with a coefficient of correlation slightly higher than those reported in the literature ($r^2 = 0.40$; France et al. 1997). In this diachronic study of Lake Geneva (surface area 582 km^2), which focused on a single large lake, this correlation was stronger, illustrating the influence of nutrient concentration on the $\delta^{13}C$ of the pelagic food web. The pattern observed in the P_{total} increase could be attributable to (*i*) a shift in the trophic position of whitefish, (*ii*) a lower fractionation rate during photosynthesis, or (*iii*) a greater contribution from atmospheric carbon, enriched in ^{13}C.

Two studies of whitefish diet were conducted: one in the early 1980s during the peak of eutrophication (Ponton and Gerdeaux 1988), and the other in 2000 (Gerdeaux and Hamelet 2001). They show no major change in diet; whitefish were still relying mainly on cladocerans. Thus, the observed pattern of $\delta^{13}C$ variation cannot have originated from a shift in the trophic position of whitefish.

In nearly all temperate lakes, primary production is phosphorus-limited, and P_{total} is a good estimation of pelagic primary productivity. Phytoplanktonic production – planktonic respiration increases with P_{total} (Del Giorgio and Peters 1993). When primary production increases, DIC decreases dramatically in the epilimnion. Fractionation by means of RuBisCO (ribulose-1, 5-bisphosphate carboxylase/oxygenase) (Raven et al. 1994) depends on the DIC concentration at the boundary layer. When the DIC stock decreases, fractionation may be reduced and may lead to a less negative $\delta^{13}C$ in the phytoplankton. Moreover, when phytoplankton production is high, the dissolved CO_2 concentration in the epilimnion drops below atmospheric saturation, resulting in a rise in pH. The very low dissolved CO_2 concentration causes a large net influx of atmospheric carbon, enriched in ^{13}C. During invasion, some of the CO_2 that enters the epilimnion is transformed into HCO_3^- (Emerson 1975). The resulting increase of ^{13}C in the pelagic food web would then be attributed to the invasion by atmospheric CO_2, enriched in ^{13}C, which compensates for the DIC fixed by photosynthesis (Schindler et al. 1973, 1997). In large lakes, eutrophication leads to a greater contribution of atmospheric carbon than of endogenous carbon.

This pattern of $\delta^{13}C$ variation with P_{total} is only valid for large lakes. For small ones, the influence of P_{total} on $\delta^{13}C$ is less clear. Benthic primary production has been shown to decrease when the lake is fertilized (Vadeboncoeur et al. 2001). However, respiration in the benthic community may actually increase, as pelagic inputs, resulting from sedimentation, are higher (Denicola et al. 2003). Moreover, in small lakes, benthic DIC makes a significant contribution to pelagic photosynthesis (Jonsson et al. 2003). The response of small lakes to eutrophication may be a combination of higher pelagic primary production plus a higher DIC contribution of benthic respiration to pelagic production.

In conclusion, the between-lake variation in whitefish $\delta^{13}C$ has important implications in terms of carbon supply to the pelagic food web. The $\delta^{13}C$ is mainly determined by lake size. In small lakes, the watershed and benthic and littoral influences on the pelagic zone are very important, supplying the pelagic food web with endogenous inorganic carbon resulting from the mineralization of allochthonous, benthic, or littoral production. With increasing size, the contributions of the watershed and littoral zone decrease, the endogenous DIC is no longer sufficient to sustain photosynthetic demand, and consequently, pelagic primary producers exploit dissolved atmospheric carbon.

Primary production, assessed from P_{total}, has less effect on the carbon source of the pelagic food web. Eutrophication increases the DIC demand of pelagic primary producers, enhancing the invasion of atmospheric CO_2 in large lakes. The response of small lakes to an alteration in trophic status seems to be more complex. However, whitefish, and indeed fishes in general, may be too mobile, moving between the littoral and pelagic zones, to be used as satisfactory models for integrating pelagic $\delta^{13}C$ in very small lakes. In this context, it could be more appropriate to use filter-feeding mollusks, such as mussels, to assess the $\delta^{13}C$ of pelagic autotrophs (Post 2002).

This study illustrates the links between allochthonous, littoral, benthic, and pelagic carbon flows via the circulation of DIC, and could provide a further argument in favor of reintegrating these habitats into future studies of food webs in lakes (Vadeboncoeur et al. 2002).

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Effects of sediment nutrients and depth on small-scale spatial heterogeneity of submersed macrophyte communities in Lake Pleasant, Pennsylvania

R.K. Johnson and M.L. Ostrofsky

Abstract: Sediment concentrations of total and available nitrogen (N), phosphorus (P), and potassium (K) and organic matter from the littoral zone of Lake Pleasant, Pennsylvania, were highly variable. Only organic matter and total N were correlated with depth, however. This result suggests the existence of more complex environmental gradients than the prevailing paradigm of monotonic changes in sediment characteristics with increasing depth. The spatial heterogeneity of submersed aquatic plant communities was significantly correlated with depth, and available N and P. Canonical correspondence analysis demonstrated that these three factors explained 38% of the variance in community structure. Other sediment characteristics (available K, organic matter, and total N, P and K) were not significant by themselves, but all variables combined explained 63% of community-structure variance. Cluster analysis identified species or groups of species typical of endpoints on the depth versus nutrient axes. *Myriophyllum exalbescens* was typical of deep sites with relatively nutrient-rich sediments, whereas deep nutrient-poor sites were dominated by *Vallisneria americana* and *Megalodonta beckii*. Shallow nutrient-rich sites were dominated by several species of *Potamogeton* and *Elodea canadensis*, and shallow nutrient-poor sites were dominated by *Heteranthera dubia* and *Najas flexilis*. These results demonstrate the importance of sediment characteristics in determining macrophytes' community structure within lakes.

Résumé : Les concentrations de azone (N), phosphore (P) et potassium (K) totaux et disponibles et de matière organique dans les sédiments de la zone littorale du lac Pleasant en Pennsylvanie sont très variables. Cependant, seuls le N total et la matière organique sont en corrélation avec la profondeur. Cette observation indique l'existence de gradients environnementaux plus complexes que de simples changements monotones des caractéristiques des sédiments en fonction de la profondeur, comme le veut le paradigme dominant actuel. L'hétérogénéité spatiale des plantes aquatiques submergées est en corrélation significative avec la profondeur et N et P disponibles. Une analyse des correspondances canoniques montre que ces trois facteurs expliquent 38 % de la variance de la structure de communauté. Les autres caractéristiques des sédiments (K disponible, matière organique et N, P et K totaux) ne sont pas significatives par elles-mêmes, mais toutes les variables combinées expliquent 63 % de la variance de la structure de communauté. Des analyses de groupement permettent d'identifier les espèces ou les groupes d'espèces typiques des points terminaux des axes des nutriments en fonction de la profondeur. *Myriophyllum exalbescens* est caractéristique des sites profonds à sédiments relativement riches en nutriments, alors que *Vallisneria americana* et *Megalodonta beckii* prédominent dans les sites profonds pauvres en nutriments. Plusieurs espèces de *Potamogeton* et *Elodea canadensis* prédominent dans les sites peu profonds riches en nutriments et *Heteranthera dubia* et *Najas flexilis* le font dans les sites peu profonds, mais pauvres en nutriments. Ces résultats démontrent l'importance des caractéristiques des sédiments pour expliquer la structure des communautés de macrophytes dans les lacs.

[Traduit par la Rédaction]

Introduction

The analysis of the density and distribution of individual organisms and of the structure of biological communities is central to ecology. The structure of submersed plant communities in lakes is of particular importance to aquatic ecologists. The nature of these communities has been shown to affect light (Ray et al. 2001), temperature (Unmuth et al. 2000), turbulence (Petticrew and Kalff 1992), water and sediment chemistry (Wigand et al. 1997), and the abundance and composition of other biotic assemblages from epiphytes (Jackson et al. 1994) to phytoplankton (Mjelde and Faafeng 1997) to invertebrates (Dvorak and Best 1982) to fish (Chick and McIvor 1994). Plant community structure is af-

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Table 1. Overview of studies seeking relationships between environmental variables and the distribution and abundance of aquatic vascular plants among lakes.

Location	No. of lakes	Primary determinants	Reference
Denmark	82	Alkalinity, pH	Vestergaard and Sand-Jensen 2000
Wales	70	Conductivity, total dissolved solids, hardness	Seddon 1972
Cape Cod, Mass., USA	5	Pore-water nutrients	Roman et al. 2001
Ireland	574	Conductivity, alkalinity, Ca, pH	Heegaard et al. 2001
Adirondacks, N.Y., USA	31	pH, alkalinity, conductivity, Ca, Mg	Jackson and Charles 1988
Adirondacks, N.Y., USA	9	pH	Roberts et al. 1985
Nova Scotia, Canada	21	Alkalinity, total P, total N	Srivastava et al. 1995
Kejimkujik National Park, N.S., Canada	20	Ca, pH, alkalinity	Catling et al. 1986
Finland	57	Conductivity	Toivonen and Huttunen 1995
Manitoba, Canada	305[a]	Alkalinity, filterable residue, pH	Pip 1979
New England, USA	321[a]	Alkalinity	Hellquist 1980
Brazil	30[a]	pH, $P_{sediment}$, P_{water}	Bini et al. 1999
Southeastern Ontario, Canada	16	Conductivity	Crowder et al. 1977
Japan	500	pH, alkalinity, Ca	Kadono 1982
Egypt	60[a]	Canal width, shading, conductivity, nutrient concentrations	Khedr and El-Demerdash 1997
Egypt	3	Altitude, Ca, Mg, NO_3, organics	Ali et al. 1995

[a]Collections from "sites" or "locations"; the actual number of lakes is not listed.

fected by history (e.g., acid rain, eutrophication, invasive species), by biotic interactions (e.g., competition, predation), and by environmental gradients (e.g., light, depth, nutrients, ice scour, turbulence). The relative importance of each to community structure, however, is often difficult to determine.

Ecologists have been successful in identifying factors controlling the structure of aquatic plant communities on a regional scale. In most of these studies, the community composition of a number of geographically proximate lakes has been found to be strongly affected by such water-quality characteristics as conductivity, alkalinity, pH, etc. (Table 1). While these studies have contributed much to our understanding of the environmental tolerances of individual species, they have not addressed the heterogeneous nature of communities within individual lakes. In fact, it has been argued that while plant communities are constrained by water chemistry on a regional scale, water chemistry cannot explain the considerable within-lake spatial heterogeneity (Duarte and Kalff 1990; Duarte and Roff 1991). Lakes with complex morphometries may, of course, have variations in water chemistries among various isolated bays and near major inflows, but for the most part, within-lake water chemistry varies little. Since it has been demonstrated that aquatic plants derive most of their nutrient requirements from the sediment (Nichols and Keeney 1976; Carignan and Kalff 1980; Barko 1982) and that plant biomass readily responds to sediment nutrient enrichment (Anderson and Kalff 1986; Duarte and Kalff 1988), an analysis of sediment chemistry, rather than water chemistry, may be a more fruitful approach in attempting to explain within-lake variations in plant community structure.

The variability of sediment quality in the littoral zone in lakes has been under-appreciated. In the littoral sediments (<3 m depth) of Canadohta Lake, Pennsylvania, Ostrofsky and McGee (1991 and unpublished data) found that the coefficients of variation of the concentrations of phosphorus (P) species ranged from 63% for organic P to 133% for NH_4Cl-extractible P. Oehm et al. (1997) found that the coefficient of variation of organic matter (loss on ignition (LOI)) was 80% and that of acid-volatile sulfides 67%. In apparently uniform weed beds in Lake Memphremagog (Quebec/Vermont), Anderson and Kalff (1986) found coefficients of variation of 41%–78% for nitrogen (N), 7%–60% for P, 13%–55% for potassium (K), and 21%–100% for organic content. Even in profundal sediments, adjacent sediment samples show spatial variation that cannot be explained by analytical error or microscale variation. Downing and Rath (1988) found between-sample variance to be 2–320 times greater than within-sample variance for a variety of sediment characteristics. The causes of littoral and profundal sediment patchiness are unknown, but might include sediment shadows in the lee of macrophytes or outcrops, ice scour and rafting, groundwater-discharge discontinuities, activities of benthic invertebrates, and currents (Downing and Rath 1988).

Studies in Lake Memphremagog and adjacent Quebec lakes (Anderson and Kalff 1988) and in Lake Geneva (Lehmann et al. 1997) examined the hypothesis that aquatic plants had specific optima with respect to sediment characteristics (e.g., sediment N, P, K, grain size, water content, depth, % C, etc.). However, neither simple regressions between sediment characteristics and biomass nor analyses of variance among the sediment characteristics of monospecific stands of plants provided supporting evidence. From the results of both studies it was concluded that sediment characteristics could not explain the patchy distribution of species within a lake. One limitation of both of the above studies is that correlation and analyses of variance assume that plant biomass and composition show unidirectional changes along resource gradients,

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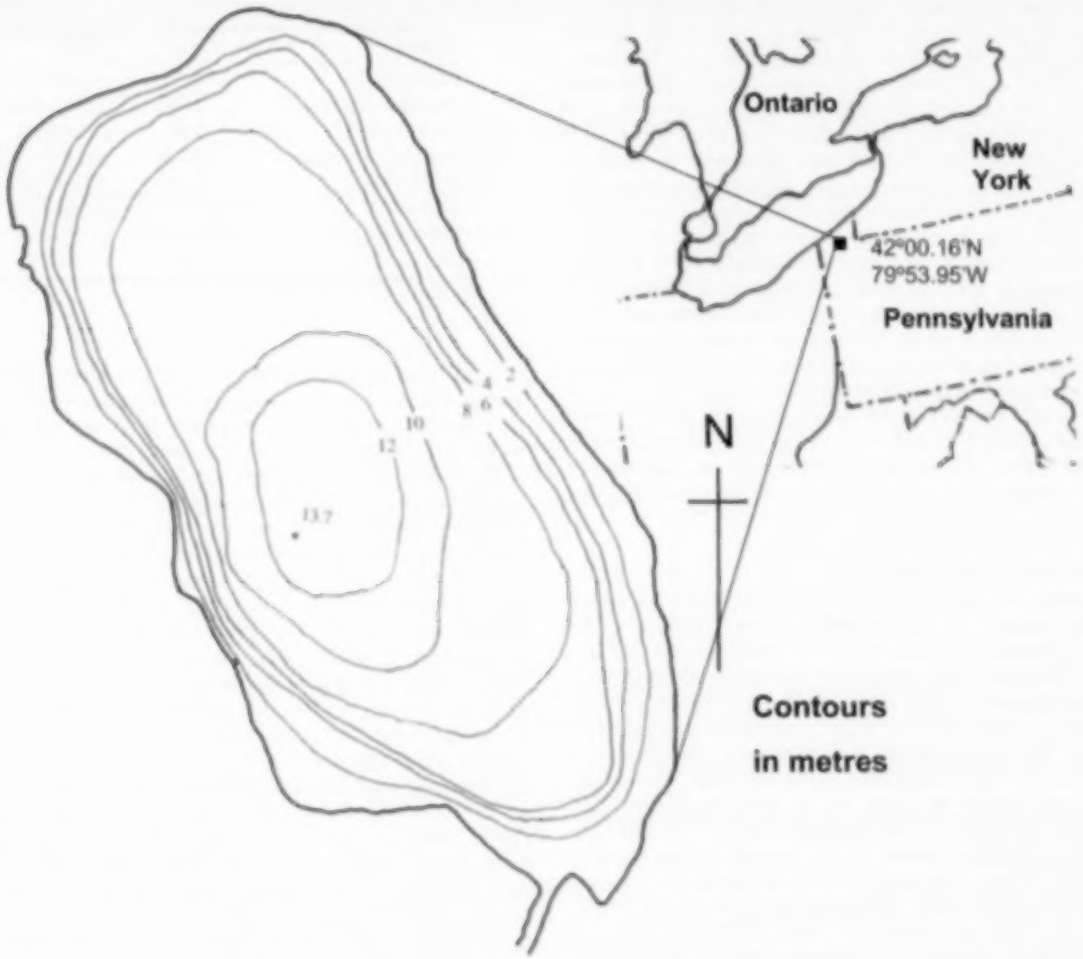
Fig. 1. Location of Lake Pleasant, Pennsylvania, USA (42° 00.16′N, 79° 53.95′W), and a bathymetric map showing the simplicity of the basin.



when in fact, species response is more likely to be unimodal. This curvilinear response to both simple and potentially complex combinations of site characteristics clouds the application and interpretation of simple statistical designs. Investigators seeking relationships between plant communities of many lakes and water chemistry have made frequent use of multivariate tools rather than simple correlations (see references in Table 1). Application of similar tools to within-lake data may help determine the response of macrophyte community structure to multiple nonlinear environmental gradients.

Here we test two hypotheses in a small lake of simple morphometry and uniform water chemistry. The first hypothesis is that the sediment environment is patchy, and nutrients vary in ways that are not explained by depth gradients. The second is that the heterogeneous environment that results from the interplay between sediment-quality patchiness and a more uniform depth gradient can explain a significant fraction of the observed spatial heterogeneity of aquatic plant communities on a local, within-lake scale.

Materials and methods

Description of study area

Lake Pleasant (Erie County, Pennsylvania, 42°00.16′N, 79°53.95′W) is a small (24 ha, 13.7 m z_{max}) meso-eutrophic (35 $\mu g \cdot L^{-1}$ total P in spring), moderately hard water (100 $mg \cdot L^{-1}$ alkalinity as $CaCO_3$), dimictic lake of simple morphometry consisting of a single symmetric basin (Fig. 1). Land use in the watershed (3.6 km^2) is currently mixed second-growth forest and light agriculture. The high total P is an apparent legacy of intense recreational activity in the early part of the last century that included a lakeside resort hotel, picnic and dance pavilions, steam-powered water ferries, a water slide, swimming beaches, etc. Current recreational impacts, however, are very low. Approximately two-thirds of the shoreline is protected by the Western Pennsylvania Conservancy, and the Pennsylvania Fish and Boat Commission has prohibited the use of motorized boats. Perhaps as a result, Lake Pleasant is the only natural lake in western Pennsylvania that has escaped both extensive lake-

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shore development and invasion by Eurasian water milfoil (*Myriophyllum spicatum*).

The western, northern, and southern shorelines of Lake Pleasant have low relief and support a rich riparian community dominated by swamp loosestrife (*Decodon verticillatus*), pickerel weed (*Pontederia cordata*), and several species of sedges (*Scirpus* spp. and *Eleocharis* spp.), out to a depth of 0.66 m (0.04 m SE). From there to a depth of 1.52 m (0.10 m SE) the plant community is a mix of *Brasenia schreberi*, *Nymphaea odorata*, and *Nuphar variegatum*. We found very little submersed plant biomass in this zone dominated by floating-leaved plants, presumably because of shading. Light measurements indicated that under these floating-leaved canopies only about 6% of surface light penetrates to a depth of 1 m. This provides a light environment equivalent to that at a depth of about 4.5 m in the absence of a canopy. A similar shading effect on submergent plants by a floating-leaved canopy has been noted in other studies (e.g., Ray et al. 2001). The eastern shore of the lake has greater topographic relief and is bounded by a road, both of which minimize the littoral transitional habitat. Only infrequently are well-developed stands of emergent or floating-leaved plants found here.

Data collection and analysis

Sampling took place in midsummer 2001. We established sampling transects at right angles to the shore at 50-m intervals. A calibrated line was swum out into the lake and anchored. Transects were sampled at 5-m intervals along this line from shore to a depth where plants were no longer present, using a metal frame with an inner sampling quadrat of 0.35 m^2. We avoided areas with extensive floating-leaved canopies. All "above-ground" plant material within the quadrat was picked by hand, and a sediment sample was taken from the center of the quadrat with a 3 cm diameter corer. Depth was determined using a measuring tape fixed to the quadrat frame. Collected plants were separated by species using Fassett (1980), Hellquist and Crow (1980, 1982, 1984), and Crow and Hellquist (1982, 1983). Dry biomass was determined following oven-drying (60 °C) to constant weight.

Cored sediments were held under refrigeration (less than 5 days) until analyzed. Available N and P were extracted from fresh sediment using 1 mol·L^{-1} LiCl and 24 h of end-to-end agitation on a shaker table (Boatman and Murray 1982). Samples were centrifuged and the supernatant was split. One aliquot was used for K analysis using a Perkin–Elmer atomic absorption apectrophotometer and the remainder was analyzed for NH_3–N using the phenate method (American Public Health Association 1995). Available P was extracted using 0.1 mol·L^{-1} NaOH – 0.1 mol·L^{-1} NaCl (Anderson and Kalff 1986) and analyzed using the molybdenum blue technique (Strickland and Parsons 1968).

Following the determination of available N, P, and K, the remaining sediment was oven-dried (60 °C) and wet/dry conversions were calculated so that the above parameters could be expressed as mass per gram sediment dry weight. Total N and total carbon (C) were determined on dry sediment with a Perkin–Elmer CHN elemental analyzer. A known weight of dried sediment (0.01–0.04 g) was digested with nitric and perchloric acids, and the resulting solution diluted to 100 mL with distilled water. Total K was determined on an aliquot with an atomic absorption spectrophotometer, and total P was analyzed on the remainder of the sample using the molybdenum blue technique (Strickland and Parsons 1968).

Table 2. Summary of water depths and chemical characteristics of sediments of sampled quadrats from Lake Pleasant, Pennsylvania.

Variable	Mean	Range
Depth (cm)	198	35–438
Available N (mg·g^{-1})	0.055	0.001–0.361
Total N (%)	0.86	nd–3.09
Available K (mg·g^{-1})	0.326	0.026–1.097
Total K (mg·g^{-1})	3.43	0.52–8.09
Available P (μg·g^{-1})	57.1	1.2–263.3
Total P (μg·g^{-1})	567.9	107.1–1309.9
Organic C (%)	13.35	1.39–37.65

Note: nd, not detectable.

From these data we constructed two matrices: site × plant species and site × site characteristics. We eliminated those quadrats without plants present (the deepest along each transect) and those species with a relative frequency less than 5%. To identify frequently occurring groupings of species we performed cluster analysis on Bray–Curtis doubly standardized (Poole 1974) plant-biomass data. The double standardization gives each species a relative importance value at each site when all species and all sites have been given equal weight. The site attributes of emergent natural groupings were compared using analysis of variance. To identify environmental factors influencing community composition, we used canonical correspondence analysis (CCA; ter Braak and Smilauer 1998; CANOCO 4, Microcomputer Power, Ithaca, New York), using both the unstandardized plant-species matrix and the site-characteristic matrix. Tests for normality led us to natural-log transform available N, P, and K. The remaining variables (depth, % C, total N, total K, and total P) were approximately normally distributed. All parameters were then normalized to a mean of zero with unit variance. A Monte Carlo test using 199 permutations was included in the CCA to test significance of the canonical axes.

Results

Overall we characterized the sediments and identified and quantified submersed aquatic plants from 103 quadrats along 18 transects. We provide a summary of the sediment characteristics of the quadrats (Table 2). Ranges of values overlapped those observed in similar studies (e.g., Lake Memphremagog; Anderson and Kalff 1986). Quadrats ranged from 35 to 438 cm in depth. Within this littoral zone, however, there was considerable variability in sediment characteristics. The most variable parameter measured was N, both available and total, with coefficients of variation of 104% and 78%, respectively. However, even the least variable parameter, P, had coefficients of variation of 67% and 36% for available P and total P, respectively. Most of the chemical characteristics were significantly correlated with each other (Table 3). The abundance of significant correlations is typical in a suite of lake-sediment characteristics

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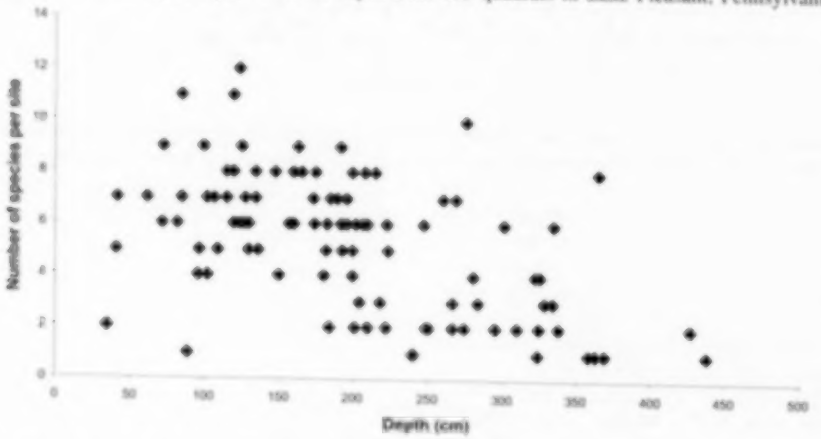
Table 3. Correlations among depths and chemical characteristics of sampled quadrats.

	% C	Total N	Total P	Total K	ln(available K)[a]	ln(available N)[a]	ln(available P)[a]
Depth	0.396	0.281	–0.051	–0.08	–0.077	–0.06	–0.123
% C	—	0.689	0.358	0.066	0.516	0.522	0.433
Total N		—	0.563	0.379	0.654	0.516	0.588
Total P			—	0.606	0.673	0.443	0.692
Total K				—	0.604	0.395	0.528
ln(available K)[a]					—	0.681	0.686
ln(available N)[a]						—	0.606

Note: At 100 df, critical $r = 0.200$.

[a]Available K, N, and P were natural log transformed to stabilize variance.

Fig. 2. Number of taxa of submersed aquatic plants versus depth from 103 quadrats in Lake Pleasant, Pennsylvania.



(Williams et al. 1976; Ostrofsky 1987). Total C and total N were significantly correlated with depth ($p < 0.005$), but total P, total K, and available N, P, and K were not.

From the same 103 quadrats we also identified 17 species of submersed aquatic plants. The assemblage was typical of moderately hard-water lakes (Moyle 1945). Quadrats contained from 1 to 12 species (average richness = 5.4). Species richness was correlated with depth ($r = -0.56$, $p < 0.001$), although scatter in the data precluded the construction of a predictive relationship (Fig. 2). Six of the plant species (*Potamogeton amplifolius*, *Potamogeton pusillus*, *Ceratophyllum demersum*, *Megalodonta beckii*, *Heteranthera dubia*, and *Najas flexilis*) had relative frequencies greater than 50% (Table 4). Plant dry biomass in quadrats varied from 0.09 to 144.62 g·m^{-2} (average = 33.7 g·m^{-2}). Maximum biomass was found between depths of 0.75 and 1.5 m (Fig. 3). *Potamogeton robbinsii*, *Potamogeton* sp., *Ceratophyllum echinatum*, and *Ranunculus longirostris* were eliminated from further analysis on the basis of low relative frequencies. The final plant-species matrix contained 99 sites and 13 species.

At a similarity of 62.5%, cluster analysis identified seven distinct groups of sites based on relative-importance values (Bray–Curtis doubly standardized) of species identified from those sites. Five of these groups were quite homogeneous; the remaining two were more mixed. Eight sites (group D; Fig. 4) were dominated by *Chara* sp. (relative importance > 65%), 17 sites (group E) by *P. amplifolius* (relative importance > 72%), 10 sites (group B) by *N. flexilis* (29% < relative importance < 99%), 6 sites (group C′) by *Myriophyllum*

Table 4. Submersed aquatic plants identified from Lake Pleasant, Pennsylvania.

	Frequency[a]	Max. biomass (g·m^{-2})	Avg. biomass (g·m^{-2})
Ceratophyllum demersum	67	26.2	3.26
Megalodonta beckii[b]	62	139.0	7.82
Potamogeton pusillus	60	75.5	4.60
Potamogeton amplifolius	60	79.6	23.37
Heteranthera dubia	56	17.1	3.74
Najas flexilis	56	12.5	1.69
Vallisneria americana	46	13.2	1.90
Potamogeton richardsonii[b]	43	27.5	4.16
Chara sp.	39	70.4	8.65
Myriophyllum exalbescens[b]	19	17.2	4.27
Potamogeton crispus	14	3.6	0.64
Elodea canadensis	14	26.2	3.22
Potamogeton zosteriformis[b]	12	3.8	1.48
Ranunculus longirostris[b]	3	1.0	0.44
Potamogeton sp.	3	1.1	0.46
Potamogeton robbinsii	2	22.4	13.14
Ceratophyllum echinatum	1	0.04	0.04

[a]The number of quadrats, out of 103 surveyed, in which a species occurred. Maximum (Max.) and average (Avg.) biomass are given in oven-dry weight.

[b]Pennsylvania Species of Special Concern (Bissel et al. 1989).

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Fig. 3. Dry-weight biomass of submersed aquatic plants versus depth from 103 quadrats in Lake Pleasant, Pennsylvania.

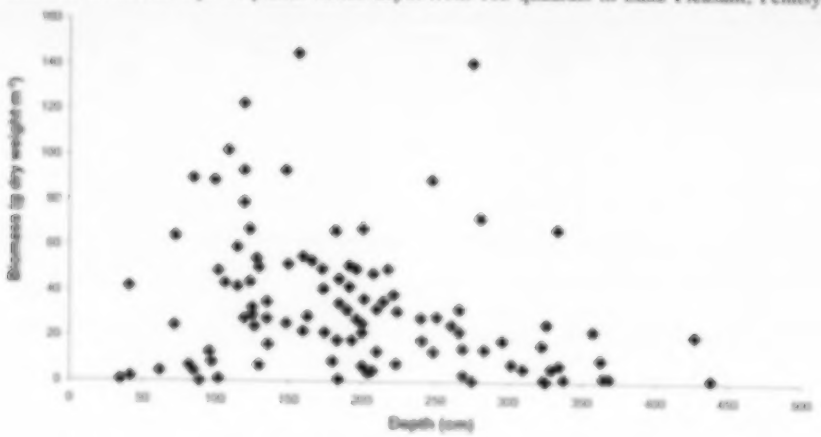
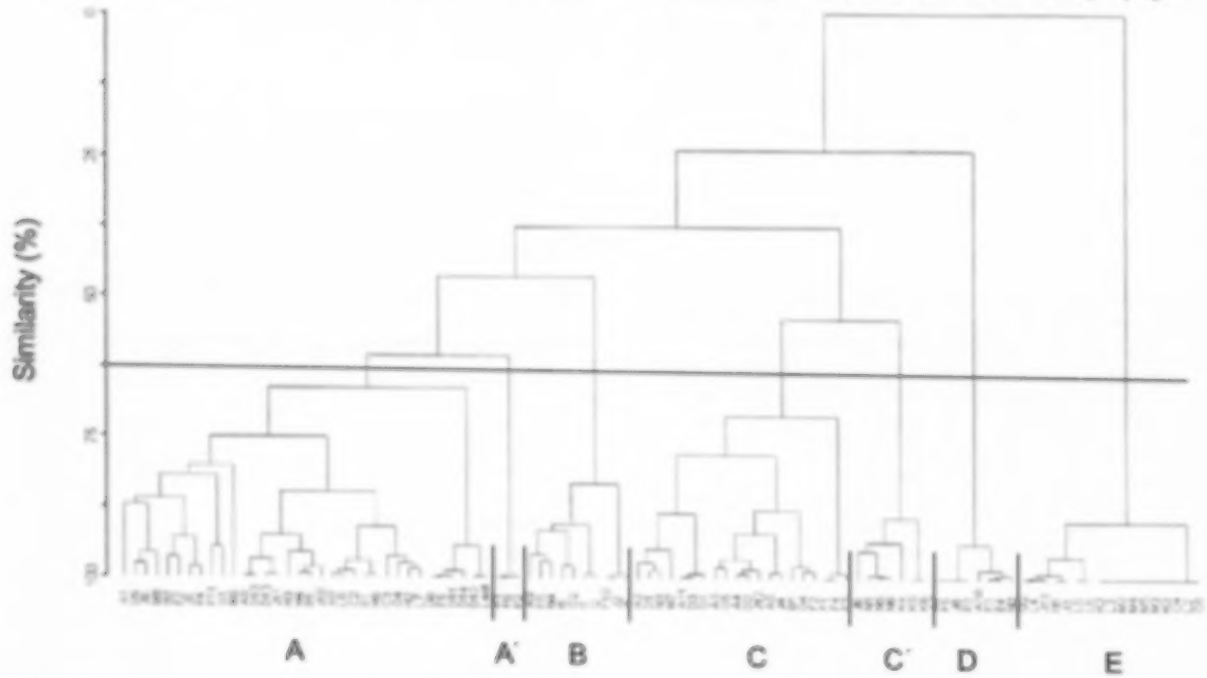


Fig. 4. Bray–Curtis similarity in the species composition of 99 quadrats in Lake Pleasant, Pennsylvania. Biomass values for the 13 most frequent species were doubly standardized. The horizontal line indicates 62.5% similarity and separates quadrats into seven groupings.



exalbescens (relative importance > 51%), and 3 sites (group A′) by *C. demersum* (relative importance > 90%). The remaining two groups (A and C) were more heterogeneous: sites in group C were dominated by one to three species of *Potamogeton* (other than *amplifolius*) and those in group A by *Vallisneria americana* or *H. dubia*.

Analyses of variance among these seven groups showed that sites from groups E, C′, and A′ had significantly ($p < 0.0001$) higher levels of organic matter than those from groups A, B, C, and D, which did not differ from each other. Sites from groups C′ and A′ were significantly ($p = 0.0018$) deeper than those from groups A, B, C, and D, and as a consequence also had lower average plant biomass. Groups A′ and C′ had significantly ($p = 0.0008$) more total N than groups A, B, C, and D. Groups C, E, C′ and A′ had significantly ($p = 0.0110$) higher available N than did groups A and B. Groups A′, E, and C′ had significantly ($p = 0.0002$) higher available P than groups D and A. There were no significant differences among the groups with respect to total P, total K, or available K. Groups D, E and A′, for which single-species relative importance exceeded 65%, had significantly lower species richness than the other groups.

We used CCA to identify important environmental gradients affecting the distribution of macrophytes. In the first ap-

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Fig. 5. Canonical correspondence analysis (CCA) biplot of (*a*) environmental factors versus sites and (*b*) environmental factors versus species. The species matrix is composed of percent stand composition by weight. Environmental factors are normalized to zero mean and unit variance. TC, total C; TK, total K; TN, total N; TP, total P; availK, available K; availN, available N; availP, available P; Cd, *Ceratophyllum demersum*; Ch, *Chara* sp.; Ec, *Elodea canadensis*; Hd, *Heteranthera dubia*; Mb, *Megalodonta beckii*; Me, *Myriophyllum exalbescens*; Nf, *Najas flexilis*; Pa, Pc, Pp, Pr, and Pz, *Potamogeton amplifolius*, *P. crispus*, *P. pusillus*, *P. richardsonii*, and *P. zosteriformis*, respectively; Va, *Vallisneria americana*.

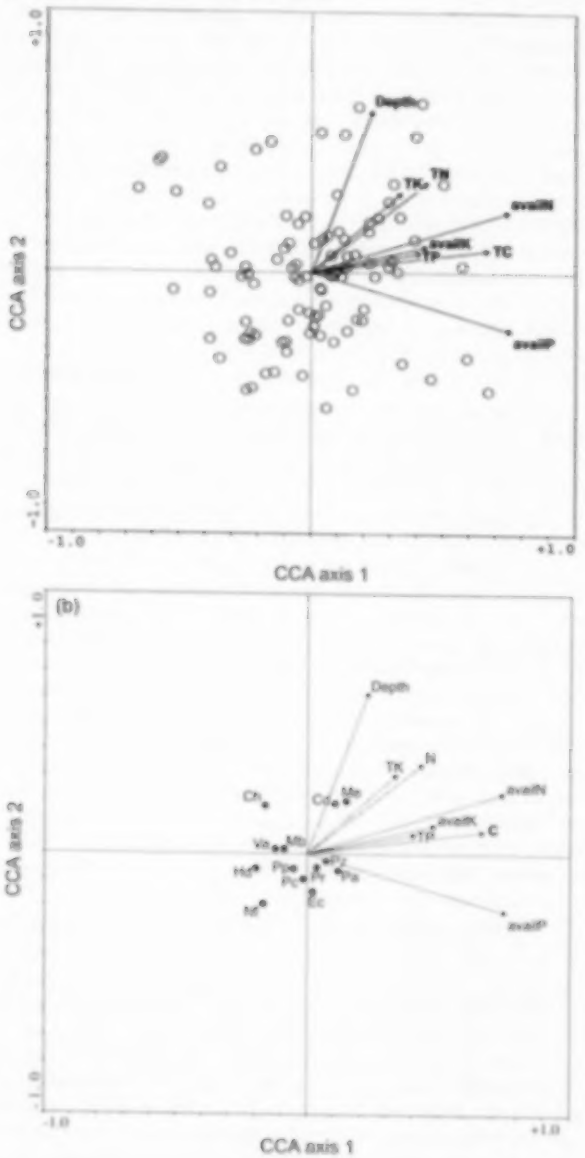

Table 5. Contribution of site characteristics to explaining the variance in species composition using stepwise forward selection.

Environmental variable	*p*	Variance explained	Cumulative variance explained
Available N	0.0100	0.16	0.16
Depth	0.0050	0.11	0.27
Available P	0.0050	0.11	0.38
Total N	0.0550	0.07	0.45
Total K	0.1300	0.06	0.51
Organic matter	0.2100	0.05	0.56
Total P	0.2900	0.04	0.60
Available K	0.9100	0.02	0.63

plication of CCA we used plant biomass in the site × species matrix. The first two CCA axes explained 69.4% of the variance in the species–environment relationship. The most important environmental factors as revealed by significant correlations with CCA axis 1 were available P ($p < 0.01$) and depth ($p < 0.01$). The most important variables correlated with CCA axis 2 were available N ($p < 0.001$) and organic content ($p < 0.001$). The variance-inflation factors of all variables were low (<4), suggesting that the high correlations among site characteristics noted above did not confound the interpretation of CCA (ter Braak and Smilauer 1998). We did, however, suspect that since depth influences community biomass quite independently of community composition, using biomass in the plant × site matrix might have given undue importance to depth in the CCA analysis. Consequently, we repeated CCA using each species' relative contribution to total site biomass rather than to biomass itself. Here the first two CCA axes explained 63.6% of the variance in the species–environment relationship ($p = 0.0100$). Sampling sites showed good separation on both CCA axes 1 and 2 (Fig. 5*a*). All measured site characteristics were significantly correlated with CCA axis 1 ($p < 0.001$ for organic matter, available N, and available P; $p < 0.01$ for total N and available K; $p < 0.05$ for total N and total K) except depth. Depth was, however, significantly correlated with CCA axis 2 ($p < 0.001$), as was total N ($p < 0.05$). We used stepwise forward selection to determine the relative contribution of each variable to the total species variance explained (Table 5). The centers of species distributions along these environmental gradients are plotted (Fig. 5*b*). *Ceratophyllum demersum* and *M. exalbescens* lie farthest along both the depth and the available-N axes, while *N. flexilis* and *H. dubia* lie in the opposite directions. Similarly, *P. amplifolius* and *Chara* sp. are at opposite ends of the available-P axis.

Discussion

There is a rich literature describing the effects of water chemistry on the composition of aquatic plant communities among lakes, and much of the variation seen in aquatic plant communities between lakes has been explained by water-quality characteristics like alkalinity, pH, conductivity, etc. However, there has been no corresponding effort to determine the cause of heterogeneous distribution of plant species within a single lake of uniform water chemistry.

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Examination of biotic interactions among species has produced no explanation for patchy distributions. Chambers and Prepas (1990) did a series of removal experiments in in-situ weed beds in Long Lake, Alberta, and asked whether plants grew better in the absence of neighbors than otherwise. They concluded that interspecific competition was slight or played only a minor role in structuring plant communities. However, they did find that dominant plant biomass was significantly correlated with abiotic factors (distance from shore, % C, exchangeable P, depth). These conclusions are supported by other similar studies. McCreary et al. (1983) used deWitt diagrams to show that interspecific effects were less important than environmental factors, and Titus and Stephens (1983) used removal experiments but were unable to show significant differences in biomass or winter bud production between plants with and without neighbors.

Investigations into the relationship between sediment characteristics and plant community structure have generally led to the conclusion that sediment characteristics could not explain community structure (Anderson and Kalff 1988; Lehmann et al. 1997), in part because of the lack of correlations between species distribution and sediment nutrient concentrations, and in part because of the prevailing paradigm that nutrients, organic matter content, particle size, light intensity, and depth vary in concert across the littoral zone. However, a few studies (e.g., Anderson and Kalff 1986; Duarte and Kalff 1988) have demonstrated that aquatic plant community biomass has responded to sediment nutrient enrichment, and the data we report here support the hypothesis that aquatic plant community structure also responds to variations in sediment nutrient concentrations and depth.

The littoral zone in Lake Pleasant extended to about 4 m in depth, with maximum plant biomass found between 0.75 and 1.5 m, likely being constrained by wave energy and available light. Within this littoral zone the ranges of all measured sediment characteristics spanned one or more orders of magnitude. Such broad ranges allow for considerable spatial discrimination of plants based on competitive interactions within particular niche optima. More significant, however, is the observation that while all nutrient concentrations were strongly intercorrelated, only C and total N were significantly correlated with depth. This result suggests that the littoral zone is better represented by a patchwork of relatively nutrient-rich and nutrient-poor sites distributed across all depths rather than a simple monotonic change with increasing depth. This increased complexity allows for a finer partitioning of the littoral zone based on both light (depth) and nutrient requirements.

Lake Pleasant has perhaps the richest submersed aquatic flora of the region, with large populations of species of special concern (Bissel et al. 1989). Here almost 64% of the variation in community structure could be explained by depth and sediment nutrient characteristics. Available N and available P were the most important of these characteristics. In the CCA biplot the distribution of the species' centroids indicates that while no species shows a preference for the extremes of any environmental gradient, *C. demersum* and *M. exalbescens* lie farthest along both the depth and the available-N axes, while *N. flexilis* and *H. dubia* lie in the opposite directions. These observations are supported by the cluster analysis, where the site groupings dominated by the former two species (groups A′ and C′) are from significantly greater depths and significantly greater available-N concentrations than are sites dominated by the latter two species (groups B and A). Similarly, *P. amplifolius* and *Chara* sp. are at opposite ends of the available-P axis, and the cluster analysis showed significant differences with respect to available P between group D (*Chara* sp.-dominated) and group E (*P. amplifolius*-dominated).

Neither *C. demersum*, an unrooted macrophyte, nor *Chara* sp., a nonvascular macroalga, can use nutrients from sediments directly. We decided not to exclude them from our analysis, however. *Ceratophyllum demersum* was the most frequently encountered species at all sites – across all depths, but with highest relative importance in the deeper sites. While it does not draw upon sediment nutrients, one of our variables was depth, and our hypothesis predicted that plant community composition would be a function of the interplay between depth and sediment nutrients. *Ceratophyllum demersum*, then, is an example of a species for which depth is far more important than sediment nutrients. Our rationale for retaining *Chara* sp. in the analysis was based on our assumption that there must be some aspect of sediment quality that discouraged the presence of rooted plants that would otherwise competitively displace *Chara* sp. In fact, sites in group D (dominated by *Chara* sp.) had significantly less organic matter, less available N, and less available P.

In general, the CCA biplot suggests that sites that are deep with nutrient-rich sediments will be dominated by *C. demersum* and *M. exalbescens*, whereas deep sites with nutrient-poor sediments will be dominated by *Chara* sp., *V. americana* and *M. beckii*. A mix of *Potamogeton* species and *Elodea canadensis* will dominate shallow nutrient-rich sites. Shallow nutrient-poor sites will be dominated by *H. dubia* and *N. flexilis*. These projections are consistent with the site differences found with cluster analysis, and largely consistent with the speculations of Chambers and Kalff (1987) and Chambers (1987), who argue that canopy/erect species (e.g., *C. demersum*, *M. exalbescens*, *P. amplifolius*) are dominant where nutrients are abundant, and bottom-dwelling species (e.g., *H. dubia*, *N. flexilis*, *Chara* sp.) are dominant where sediments are infertile. The observation that depth and sediment nutrient concentrations are not significantly correlated suggests that at any particular depth, both nutrient-rich and nutrient-poor patches will exist, supporting different communities of plants across a spatial scale determined by nutrient patch size.

Large-scale heterogeneity in the distribution of nutrients in profundal sediments and its causes are well known (Hilton et al. 1986). The causes of fine-scale heterogeneity are less well understood, even as such heterogeneity is becoming more widely appreciated. There have been, as yet, no studies to estimate resource patch size, although work in the profundal zone (Downing and Rath 1988) suggests that patches are small rather than large, on the order of metres. Littoral patches may be even smaller because they are influenced by such localized phenomena as minor topographical irregularities causing sediment shadows, ice action, upwelling groundwater, and activities of biota. Patchiness in nutrients across the littoral zone independent of depth can thus promote conditions favorable to a diverse assemblage of

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submersed plant species. Given the biotic assemblages and environmental factors that submersed aquatic plants have been shown to influence (e.g., Jackson et al. 1994; Unmuth et al. 2000; Ray et al. 2001), their local spatial heterogeneity has the potential to influence ecosystem structure and function on a variety of scales within a lake. Knowledge of factors affecting macrophyte community structure from a combination of both past regional-scale multi-lake studies and smaller scale, within-lake studies can provide a valuable set of data for predicting and interpreting macrophyte influence on other lake biotic communities of economic or conservation concern. In the future a more intimate knowledge of the major factors affecting habitat heterogeneity at different scales will enable scientists and managers to better understand the temporal changes in species composition and richness in both disturbed and undisturbed aquatic systems.

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Importance of landscape variables and morphology on nutrients in Missouri reservoirs

J.R. Jones, M.F. Knowlton, D.V. Obrecht, and E.A. Cook

Abstract: The proportion of cropland cover in the catchments of Missouri reservoirs, a surrogate for non-point-source nutrient loss from agricultural watersheds, accounts for some 60%–70% of the cross-system variance in long-term averages of total phosphorus and total nitrogen (n = 126, ln transformation for nutrients and logit for cropland). The addition of dam height and an index of flushing rate improved r^2 values to ~77% for both nutrients. Even among reservoir catchments with >80% grass and forest cover, cropland accounted for most of the variation in nutrients. Reservoir nutrients showed a strong negative relation to forest cover. Relations between grass cover and nutrients were positive but weak, and grass had no significant statistical effect once cropland was taken into account. Residual analysis suggests that urban reservoirs would have about twice the nutrient level of reservoirs in non-cropland basins (forest and grass). The increase in nutrients with the proportion of cropland and the decrease with forest cover have previously been documented in Missouri streams.

Résumé : La proportion des terres agricoles dans les bassins versants des réservoirs du Missouri, une variable de remplacement pour les pertes diffuses de nutriments dans les bassins versants agricoles, explique environ 60 % – 70 % de la variances des quantités moyennes à long terme de phosphore total et d'azote total dans les bassins (n = 126, transformation ln des valeurs de nutriments et transformation logit dans le cas des terres agricoles). L'addition de la hauteur des barrages et d'un indice de vidange améliore les valeurs de r^2 à ~77 % pour les deux variables de nutriments. Même dans les bassins versants de réservoirs avec >80 % de couverture de prairie ou de forêts, les terres agricoles expliquent la plus grande partie de la variation des nutriments. Il y a une forte relation négative entre les nutriments dans les réservoirs et la couverture forestière. Les relations entre la prairie et les nutriments sont positives, mais faibles, et tout effet statistiquement significatif disparaît lorsqu'on tient compte des terres agricoles. Une analyse résiduelle indique que les réservoirs urbains auraient environ le double des concentrations de nutriments des réservoirs dans les bassins versants sans terres agricoles (donc de forêts et de prairies). L'augmentation des nutriments en fonction de la proportion des terres agricoles et leur diminution en fonction de la couverture forestière avaient déjà été démontrées dans les cours d'eau du Missouri.

[Traduit par la Rédaction]

Introduction

A central paradigm of modern limnology is that external nutrient loading, modified by morphology and hydrology, determines the trophic state of a lake (Edmondson 1961; Vollenweider 1975). Increased biological production resulting from nutrient enrichment is a major theme in freshwater ecology (Likens 1972; Smith 1998), and nutrient control to reduce excessive productivity is the principal focus of applied limnology (Sas 1989; Cooke et al. 1993). Anthropogenic activity has accelerated eutrophication, and lake management has typically addressed this problem by reducing excessive nutrient loading associated with point-source discharge from municipalities. This approach been successful in reversing eutrophication in Lake Washington (Edmondson 1994), in areas of the Laurentian Great Lakes (Nicholls et al. 2001), in several major European lakes (Sas 1989), and in other areas.

Recently, aquatic scientists have determined that non-point-source nutrient inputs from agricultural and urban sources are a leading cause of the nation's remaining water quality problems (Novotny and Chesters 1989; Soranno et al. 1996; Carpenter et al. 1998). Studies have quantified the interdependence of land cover and nutrient export coefficients from a variety of landscapes modified by human activity (Beaulac and Reckhow 1982; Frink 1991). It can be inferred from paleolimnological records and historic water-quality data that lake enrichment, by way of non-point-source mechanisms at the landscape level, has resulted from conversion of land from native cover to agriculture and urban use (Stoermer et al. 1993; Schelske and Hodell 1995;

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Reavie and Smol 2001). Specific studies have linked changes in lakes to intensified land-use practices within their catchments; in these examples the pathway for increased nutrient and organic-matter loading was from non-point sources (Mitchell and Galland 1981; Soranno et al. 1996; Carignan et al. 2000).

Limnological research in Missouri has demonstrated that stream nutrient levels are tied to land cover through non-point processes (Smart et al. 1985; Perkins et al. 1998; Lohman and Jones 1999). The general pattern is that nutrient levels increase in streams as a function of the proportion of cropland within the watershed and decline with forest cover. Relative to forest, row-crop agriculture represents a major disturbance to the landscape, with frequent tillage and fertilizer application (Turner and Rabalais 1991; Howarth et al. 1996). Missouri analyses suggest that these two contrasting cover types account for much of the measured variance in nutrient levels among streams within the state.

In this paper, we extend the land cover nutrient analysis to Missouri reservoirs, which vary from oligo- to hypereutrophic (Jones and Knowlton 1993). Few reservoirs in Missouri have point-source inputs, so quantifying the link between land cover (an indirect measure of external nutrient input from non-point-source anthropogenic activities) and large-scale patterns of reservoir trophic state is essential for interpreting factors regulating regional water quality (Jones and Knowlton 1993). Our objective was to determine whether land cover in the watershed, and measures of morphology and (or) hydrology, could account for among-system variation in reservoir nutrient levels within the state. Our approach is consistent with the concepts that underpin simple empirical loading models (Edmondson 1961; Vollenweider 1975). We use land cover as a surrogate for nutrient input, with the supposition that cropland will be the dominant source of external nutrients. In this large-scale comparative lake study we are identifying the influence of watershed characteristics on reservoir limnology (Jones et al. 1998), and the effects of unmeasured variables remain as residual error. Surprisingly, few studies have linked land cover to lake trophic state and there is only one study of this nature on reservoirs (Knoll et al. 2003).

Methods

Limnology data

Limnology data used in this analysis come from 135 Missouri reservoirs that represent the range of reservoir resources within the state, including those used for water supply, recreation, and multipurpose Corps of Engineers reservoirs (Fig. 1). Reservoirs were sampled seasonally on three or four occasions during May–August from the surface layer at a site near the dam. Individual reservoirs were represented in the data set by collections ranging from 4 to 21 summer seasons during the period 1978–2002; most reservoirs were represented by data from ≥10 seasons. To limit the effects of temporal variation (Knowlton et al. 1984) on this analysis we confined our study to those reservoirs with four or more summer seasons' data. Samples were processed by standard methodology (Knowlton and Jones 1995). Analyses are based on lake means for total phosphorus (TP) and total nitrogen (TN) (Table 1). Lake means were calculated as nested averages over the period of record for each reservoir by calculating the geometric mean (ln-transformed) for each summer and then calculating the geometric mean across all summers to estimate the lake mean. Morphometric variables (volume and dam height) were provided by the Missouri Department of Natural Resources. Bathymetric maps were available for 26 reservoirs. For this subset, mean depth and dam height were strongly correlated ($r = 0.96$), with mean depth averaging about one-fourth of dam height. A hydrologic flushing index was estimated for each reservoir by using the regional runoff coefficient (Missouri Department of Natural Resources 1986), watershed area, and reservoir volume.

Watershed data

Geographic Information Systems and remote-sensing techniques were used to characterize cover types within the watersheds of Missouri reservoirs (forest, cropland, grass (which includes pastures), urban area, and water). Watersheds were digitized in a heads-up fashion using ESRI's Arc Info software (Environmental Systems Research Institute 1997) and United States Geological Survey 1:24 000 topographic maps in digital raster graphic format. Topology was built for each digitized watershed and a grid coverage (30 m × 30 m) was created using Arc Info software. Streams within the watersheds were digitized in the same fashion as the watersheds. The arcs depicting streams were buffered at two different distances, to create polygons around the streams that represented riparian zones of 75 and 150 m. Topology was built for the buffered streams and grid coverages were created (30 m × 30 m). Watershed and buffered-stream coverages were then imported into ERDAS IMAGINE software (Leica Geosystems GIS & Mapping 1997) and masked with a land-use coverage (1993 data) created by the Missouri Resources Assessment Program. A report was created for each masked coverage, providing the area classified in each cover-type category. The total area that was classified as water was divided into reservoir and non-reservoir categories.

Relations between landscape variables and nutrients were examined by least-squares methods of single and stepwise multiple regression with $p < 0.01$ unless otherwise stated. Data were transformed using ln or logit (adding 0.003 to cover types measured to avoid zero values) where appropriate. All analyses were performed with SPSS® for Windows version 11 (SPSS Inc. 2001).

Results

Reservoir and watershed characteristics

The median Missouri reservoir in this analysis is eutrophic, with 705 $\mu g \cdot L^{-1}$ TN and 39 $\mu g \cdot L^{-1}$ TP. Among the study reservoirs, however, nutrient values ranged 12- to 30-fold (Table 1), TP being more variable than TN (coefficient of variation = 73% vs. 44%).

The median watershed had 31% grass, 24% forest, 13% cropland, and <1% urban area, but individual proportions ranged from zero to >74% in each cover type (Table 1). Collectively, forest and agriculture (cropland plus grass) jointly composed >85% of the land area in most (80%) study basins (Fig. 2*a*), the remaining area being classified as water (median 5%) and urban area. Some 80% of the catchments had

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Fig. 1. Map of Missouri, USA, showing the location of the 135 reservoirs considered in this study.

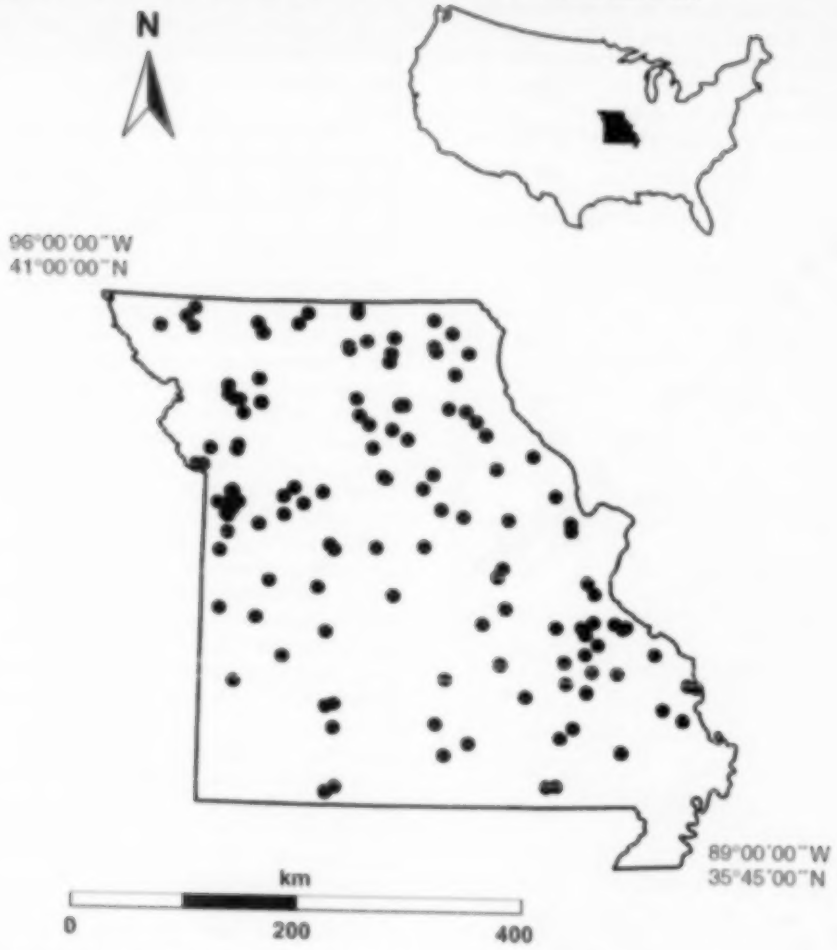

Table 1. Summary statistics for limnological data, land cover, and watershed–morphology data for Missouri reservoirs (n = 135).

	Median	Mean	Minimum	25%	75%	Maximum
Nutrient data						
Total phosphorus ($\mu g \cdot L^{-1}$)	39	45	6	21	58	182
Total nitrogen ($\mu g \cdot L^{-1}$)	705	725	200	500	920	2 330
Land cover (%)						
Forest	4	35	0	12	54	95
Grass	31	32	0	19	46	78
Cropland	13	19	0	5	32	74
Urban area	0	7	0	0	3	96
Water	5	6	0	3	8	25
Watershed–morphology data						
Reservoir area (ha)	42	750	2	17	114	21 787
Dam height (m)	14	16	5	10	19	77
Volume ($m^3 \times 10^4$)	208	7 787	6	67	509	333 319
Watershed area (ha)	1028	37 781	33	393	3857	1 875 178
Ratio of watershed to reservoir area	21	48	4	15	39	592
Flushing index ($year^{-1}$)	1.1	3.7	0.1	0.5	2.5	87.1

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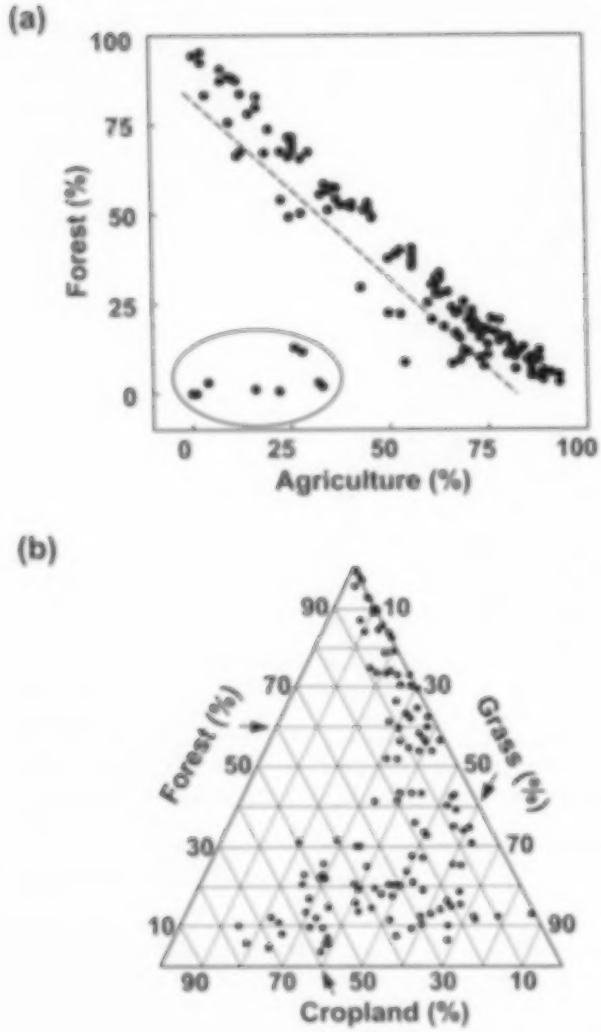

Fig. 2. (*a*) Plot of the proportion of forest cover in the catchments of 135 Missouri reservoirs against the proportion of the catchment in agriculture (cropland plus grass). The nine data points enclosed by an ellipse have >50% urban area in the catchment. The broken line represents 85% land cover jointly in forest and agriculture. (*b*) Ternary diagram showing the proportions of cropland, forest, and grass in the catchments of the Missouri reservoirs.

<5% urban area, but nine reservoirs located within metropolitan Kansas City had 50–96% urban area (mostly residential; Fig. 2*a*); this unique subset is treated separately in the land cover – nutrient analysis. Forest and grass jointly composed 75–99% of the catchment area in half of the basins (Fig. 2*b*); within this subset these two cover types were negatively correlated ($r = -0.96$, $n = 66$) and across the continuum of possible combinations, forest and grass were well represented (low, high, and equal proportions of each type). Grass and cropland jointly composed 75–93% of the catchment area in ~20% of the basins (Fig. 2*b*) in combinations of 20–70% of either cover type, which were negatively correlated ($r = -0.95$, $n = 32$). Forest showed a hyperbolic relation to cropland ($r = -0.86$, logit-transformed, urban reservoirs excluded); with the exception of a few highly forested catchments, combinations of these two cover types did not dominate the study basins.

Among catchments with >5% cropland ($n = 82$) the proportion of cropland within the 75-m corridor consistently averaged about 20% less than within the overall watershed. Similar minor differences were found among catchments such that cropland within the 75- and 150-m corridors was highly correlated with cropland in the entire drainage basin ($r \geq 0.89$, $n = 108$). Comparisons also showed that the proportion of each cover type in the riparian zone was similar to its proportion in the entire basin (grass, forest, and urban area, $r \geq 0.85$). These strong correlations limit the suitability of the data set to test the role of riparian land cover on reservoir nutrients at this scale of analysis.

There are strong correlations among the physical features of reservoirs and their watersheds (ln-transformed, $n = 135$; Table 1). Dam height was significantly correlated with reservoir surface area ($r = 0.71$), volume ($r = 0.83$), and watershed area ($r = 0.57$). Reservoir surface area was correlated with both watershed area ($r = 0.89$) and storage volume ($r = 0.96$). The ratio of watershed area to reservoir surface area (both in hectares) ranged from 4 to 592, with a median of 21 and an average of 48. The flushing index, expressed as the ratio of average inflow volume to reservoir volume, ranged from 0.1 to 87, with a median of 1.1 and mean of 3.7 (year^{-1}).

Limnological characteristics and land cover

As expected, both TP and TN in Missouri reservoirs were positively related to the proportion of cropland within their watersheds ($r > 0.61$, $n = 126$, which does not include the nine reservoirs with >50% urban area; Figs. 3*a* and 3*b*), with a pattern of increasing variance with increasing cover. Minimum nutrient levels were strongly influenced by cropland; reservoirs with >50% cropland had minimum TP and TN of 43 and 830 μg·L^{-1}, respectively. Nutrient concentrations were also weakly correlated with grass (Figs. 3*c* and 3*d*), but minimum values were low over the entire range in the data set. Both nutrients were negatively correlated with forest ($r > -0.59$; Figs. 3*e* and 3*f*), and variation declined with increasing forest. For reservoirs with >90% forest, TP and TN were less than 15 and 335 μg·L^{-1}, respectively, with little among-system variation. These results parallel the pattern seen in Missouri streams, where cropland tends to be the largest source of nutrients and forest the smallest (Perkins et al. 1998). Grass is an intermediate nutrient source, but is more similar to forest than to cropland, at least in terms of minimum observed concentrations. Neither nutrient showed a significant correlation with the proportion of urban area; reservoirs with >50% urban area had nutrient levels of 16–55 μg·L^{-1} TP and 390–900 μg·L^{-1} TN, which rank low to intermediate within the overall data set.

When transformed variables (ln for nutrients and logit for land cover) were used, cropland accounted for 62% and 71% of the variation in TP and TN, respectively ($n = 126$, not including reservoirs with >50% urban area; Fig. 4, Table 2). Multiple regression showed that the inclusion of dam height (ln-transformed), a surrogate term for lake morphometry and

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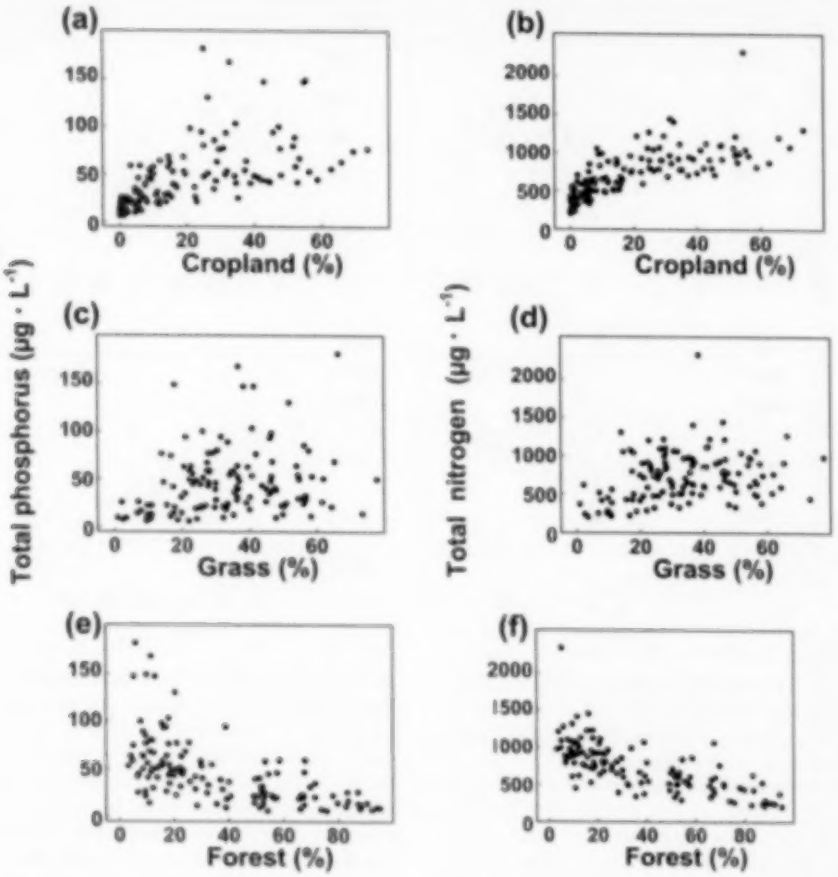
Fig. 3. Linear plots of total phosphorus and total nitrogen against the proportions of cropland, grass, and forest in the catchments.



a correlate of watershed physiography, improved the r^2 values to 73% for TP and 76% for TN (Table 2).

The addition of the flushing index (ln-transformed) improved the explanation of among-system variation in TP to 77% (Table 2) but was not significant in the TN analysis. Among these independent variables, only dam height and flushing index were significantly correlated ($r = 0.38$, $p < 0.0001$). Analysis of multicollinearity showed that parameter estimates were not adversely affected in regressions that included both dam height and flushing index. Given the intercorrelation among the physical and morphological features of these systems, watershed area (ln-transformed, $r^2 = 0.78$) or the ratio of watershed to reservoir surface area (ln-transformed, $r^2 = 0.77$) performed similarly to the flushing index in the TP analysis.

Collectively, morphology variables, and for TP, hydrology variables, accounted for ~20%–40% of the variance not accounted for by non-point-source features of cropland (Table 2). Adding other land-use categories to these models did not appreciably reduce the residual variance (only ~1% improvement in r^2 values) and were not always significant over just cropland and morphology. Even among reservoir systems dominated by grass and forest (<20% cropland, n = 75), cropland accounted for >50% of the variation in TP (52%) and TN (57%), and adding dam height improved the models to ~70% for both nutrients.

Reservoir nutrients were negatively related to proportion of forest (logit-transformed, r^2 = 0.49–0.62; Fig. 4), and with dam height and watershed area included, multiple regression explained ~70% of the among-system variation in nutrient content of the Missouri reservoirs (models not shown). Relations of grass (logit-transformed) with nutrients were positive but much weaker (r^2 = <0.2) than those with cropland or forest, and multiple regressions using the proportion of agricultural land in the watershed (cropland plus grass) explained less variance than did cropland alone. Relations with the proportion of urban area were not significant.

For the nine reservoirs with >50% urban area, the statewide regression models consistently underpredicted TP and TN. Residuals (observed minus predicted) were nearly all positive (Fig. 5) and were strongly correlated with the proportion of urban cover (r = ~0.9 for models 3 and 5 from Table 2). This result suggests that urban catchments export proportionately more TP and TN than other non-cropland cover types (forest and grass).

For non-urban catchments with cover-type measurements in the riparian corridor (n = 99), residuals from the statewide models were only weakly related to land use in the 75- and

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Fig. 4. Total phosphorus and total nitrogen plotted against the proportions of cropland and forest. Nutrients are ln-transformed and cover type was logit-transformed.

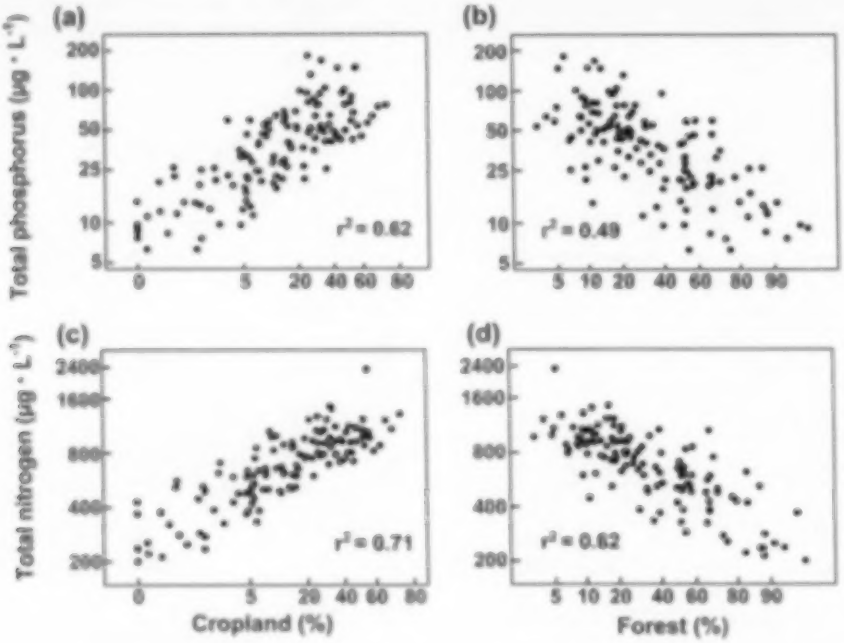

Table 2. Regression models for total phosphorus and total nitrogen (TP and TN, respectively, ln-transformed) based on the proportion of cropland (%crop, logit-transformed), morphology (dam height, DH), and hydrology (flushing index, FI).

Relation	r^2	SE
1: TP = 4.27 + 0.36 %crop	0.62	0.47
2: TP = 5.53 + 0.33 %crop − 0.50 DH	0.73	0.40
3: TP = 5.20 + 0.35 %crop − 0.37 DH + 0.12 FI	0.77	0.37
4: TN = 6.96 + 0.24 %crop	0.71	0.26
5: TN = 7.51 + 0.23 %crop − 0.22 DH	0.76	0.23

Note: Model number, standard error (SE), and coefficient of determination (r^2) are provided for each regression. Units are shown in Table 1.

150-m corridors. Residuals from the TP and TN models (models 3 and 5 from Table 2) were positively correlated with grass in the 150-m corridor (r = 0.27–0.31, $p < 0.05$), residuals from the TN model (model 5 from Table 2) were also correlated with grass in the 75-m corridor (r = 0.26, $p < 0.05$), and residuals from the TP and TN models were correlated with urban cover in the 150-m corridor (model 5 from Table 2, r = 0.2, $p < 0.05$). Proportions of forest and cropland in the riparian corridor had no significant influence on residuals from any of the models.

Discussion

Collectively, these empirical analyses specific to Missouri reservoirs support limnological theory in that nutrient concentrations are largely determined by external inputs as modified by morphology and hydrology (Edmondson 1961; Vollenweider 1975). In this statewide analysis, cropland accounts for some 60–70% of the variance in reservoir nutrient concentration. These relations with cropland were expected, but are surprisingly powerful given that they are limited to a single catchment feature, a surrogate of the degree of non-point-source loading. The models presented herein ignore nutrient contributions from non-cropland cover, which account for >75% of the land area considered in this study. The pattern, however, directly parallels findings that cropland was highly correlated with nutrients in Missouri streams (Perkins et al. 1998).

Undoubtedly, cropland is a greater relative source of nutrients than the other dominant cover types in our analysis, grass and forest. Even among reservoirs where cropland composed <5% of the basin (n = 32, urban reservoirs excluded), variation in cropland was a much stronger correlate of TP and TN than variation in other cover types. Row-crop agriculture represents a continuous disturbance to the landscape that is intensively managed by tilling, harvest, and application of nitrogen-rich fertilizers (Turner and Rabalais 1991; Howarth et al. 1996). Researchers have consistently found nutrient export from cropland to be several times that from grass and forest (Beaulac and Reckhow 1982; Frink 1991), and our analysis supports this pattern. Among Missouri reservoirs, TP and TN increased strongly with cropland and decreased with forest, resulting in about a 7-fold minimum difference in nutrients between a reservoir dominated by forest and one dominated by cropland. Regression equations based on forest cover and morphology were slightly more variable than those based on cropland but suggest that this land cover type was the smallest nutrient source in our catchments.

The influence of grass on reservoir nutrient levels was less apparent. Reservoirs in catchments dominated by grass had

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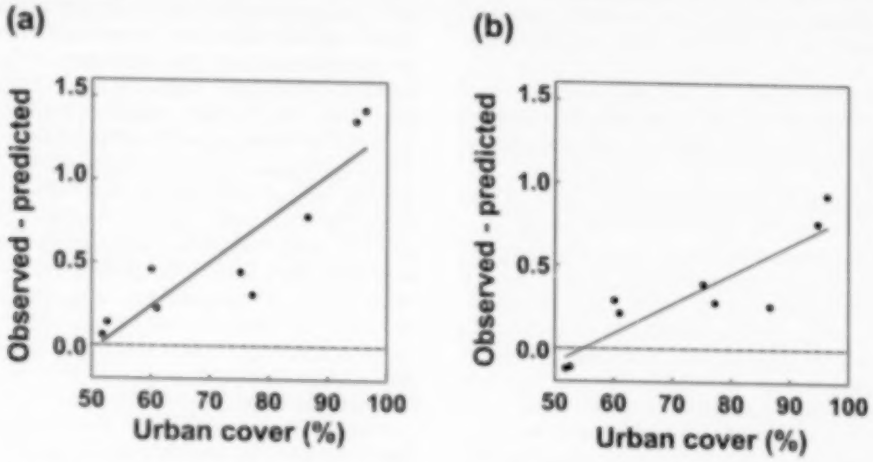
Fig. 5. Effect of the proportion of urban cover on residuals (observed – predicted, ln-transformed data) from models 3 (*a*; $r = 0.91$) and 5 (*b*; $r = 0.89$) in Table 2 calculated for nine urban reservoirs not included in the statewide land cover – nutrient analysis. Solid lines were fitted by least squares.



about triple the TN and less than double the TP of those dominated by forest, suggesting that exports from grass were intermediate between those from forest and cropland. The literature suggests that nutrient flux from grass is not necessarily uniform. Losses are much greater from intensively fertilized and grazed pastures relative to grass fields set aside for conservation (Sharpley et al. 1994; Watson and Foy 2001). This entire continuum of grassland management is known to occur within Missouri, but data from specific basins are not available. In our analyses, variation in grass had no significant statistical effect once cropland was taken into account. This finding suggests that nutrient export from grass is consistently low relative to that from cropland or that loss rates from grass are strongly correlated with those from cropland among the various catchments. Cropland in Missouri is predominantly located in regions of rich soils (Jones and Knowlton 1993), and nutrient flux from agricultural areas (cropland plus grass) in a given basin may be highly influenced by ambient soil fertility; however, we cannot test this viable hypothesis with our data set.

Nutrient export from urban catchments often equals or exceeds that from agriculture (Beaulac and Reckhow 1982; Frink 1991), and impervious surfaces increase runoff relative to other cover types. Most of our catchments had <5% urban area, but nine reservoirs in metropolitan Kansas City were unique, with >50% urban cover, and were excluded from the statewide analysis. Compared with models based on the proportion of cropland in the catchment these reservoirs had higher TP and TN than predicted, the difference increasing directly with the proportion of urban cover. Residual analysis suggests that a reservoir in an urban catchment (zero cropland) would have twice the nutrient level of a reservoir in a non-cropland basin (forest and grass) represented in our statewide regressions (e.g., ln residual >0.69). Data from Missouri streams support this pattern (Smart et al. 1985). This preliminary analysis suggests that there are strong effects of urbanization on reservoir nutrients, but most Missouri impoundments are in rural regions where urban cover is a minor component of land cover.

In this analysis the percentage of cropland is a surrogate for nutrient concentration in the inflowing streams (Perkins et al. 1998). In steady-state models, lake nutrient concentrations are a function of inflow values minus sedimentation (Vollenweider 1975). Sedimentation is governed by several physical processes such as settling velocity, settling distance (mean depth), time available for settling to occur (flushing rate), and several biological processes such as zooplankton feeding and resuspension by bottom-feeding fish. In this presentation dam height serves as a surrogate for mean depth and is a correlate of reservoir volume, stratification potential, and hydrology. Flushing index is inflow volume relative to reservoir volume and is correlated with watershed area and the ratio of watershed area to lake surface area. In all cases these physical metrics explained additional variance in reservoir nutrients not accounted for by cover type.

Loss of nutrients as a result of sedimentation should decrease with increasing flushing rates, making flushing a positive influence on in-reservoir nutrient levels. Consistent with this expectation, the coefficient for the flushing index is positive (Table 2, model 3). For a given flushing rate and inflow concentration, the expected effect of increasing lake depth is also positive (Cooke et al. 1993). With increasing water-column depth there is a decreasing probability that sedimenting particles will reach the bottom before water exits the lake. In our regression models, however, the coefficients for depth (dam height) differ by being negative. For example, based on model 3 the median Missouri reservoir (13% cropland, dam height 14 m, and flushing index 1.1) would have 36 $\mu g \cdot L^{-1}$ TP, but when other features are held constant, a reservoir with half that dam height would have 46 $\mu g \cdot L^{-1}$ TP and a reservoir with twice the dam height would have 28 $\mu g \cdot L^{-1}$ TP. Internal nutrient loading is an inverse function of mean depth (Nürnberg 1984) and may contribute to this apparent disparity between our results and convention. Also, inputs to reservoirs are often affected by plunging inflows, yielding interflow or underflow currents that deliver incoming nutrients to subsurface strata with little effect on the surface conditions reflected in our data (Knowlton and Jones

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1995). The phenomenon is likely of greater consequence in deeper water bodies relative to shallower ones, and this inflow pattern likely contributes to the large coefficients used to describe sedimentation processes in reservoirs relative to natural lakes (Jones and Bachmann 1978; Canfield and Bachmann 1981). We cannot quantify the role of either process with these data, but nearly all Missouri reservoirs develop subsurface anoxia during stratification, thereby increasing the potential for internal loading, and plunging inflows are common.

Several landscape-level factors, outside the scope of this analysis, likely contributed to unaccounted-for variation in our relations. Among these, variation in rates and timing of fertilizer application and tillage practices, all major factors in determining yields (Howarth et al. 1996; Baker and Richards 2002; Richards et al. 2002), would have contributed to non-uniform losses from agricultural fields (both cropland and grass). Changes in land use during the study period would also have contributed to residual error. In addition, the spatial pattern of land cover within the catchments, referred to by Johnson et al. (1997) as patch density, would be a source of additional variation in chemical flux from catchments (Soranno et al. 1996).

Land use within the riparian zone can be a critical factor in determining nutrient export from a watershed. Land away from the stream channel is thought to have less impact on stream nutrients, and hence flux of materials to downstream reservoirs, than land close to the channel (Osborne and Wiley 1988). We had expected that our characterization of land use within the riparian zone of these basins would be a significant factor in our models. Our data, however, are not well suited for quantifying the effects of vegetated buffers because of the strong correlation between the major cover type in the entire catchment and that found in the riparian zone. Although most watersheds had a larger proportion of forest and grass relative to cropland in the riparian corridor (median values within the 75-m corridor were 42% forest, 31% grass, and 10% cropland), the range of conditions in our data set was too narrow to provide a strong test of riparian buffers. Others have quantified the attenuation of nutrient export by vegetated buffers (Osborne and Kovacic 1993), whereas in some large-scale studies there is no evidence of reduction (Omernik et al. 1981).

Volatilized nitrogen from fertilizers and animal-waste facilities within the state could be an unmeasured atmospheric source of nitrogen to the basins and directly to the reservoirs (Howarth et al. 1996). Biotic factors may also influence among-system variance though sediment-feeding fish (Michaletz 1997; Schaus et al. 1997) that would contribute to internal loading. In two reservoirs, known introductions of grass carp (*Ctenopharyngodon idella*) have reduced littoral vegetation, with concurrent increases in pelagic nutrients and algal biomass (J. Jones, unpublished data) during a period when the proportion of cropland in both catchments decreased. Several reservoirs were intentionally fertilized to improve the fishery, but removing these systems from the analysis resulted in only small improvements in cover type – nutrient relations. Several reservoirs receive inputs from municipal effluents, but this information did not improve the models. Lastly, our limnological collections are from the down-lake zone of these impoundments, near the dam. They represent conditions after in-reservoir processes such as sedimentation, uptake, and dilution have altered the chemistry and suspended-solids content of inflow from the catchment (Jones and Knowlton 1993), thereby blunting the relation between nutrient flux from the catchment and reservoir measurements. Surrogate measures of morphology and hydrology, dam height, and flushing accounted for variance attributed to these processes in our models.

Our land cover – nutrient relations, modified by physical features, match or exceed the level of explanation provided by similar cover-type relations in Connecticut lakes (Field et al. 1996), where relations were negative with forest and positive with urban cover and agriculture, Ontario (Dillon and Molot 1997), where peatlands explained among-lake variation in TP, Quebec (Carignan et al. 2000), where forest harvest was important in determining TP, Alberta (Prepas et al. 2001) where wetlands were correlated with TP, and Ohio (Knoll et al. 2003), where agriculture explained variation in maximum TP among 12 reservoirs. Similarly, Meeuwig and Peters (1996) successfully used empirical land-use models based on catchment characteristics and morphometry to model chlorophyll in a broad suite of lakes. Predictions of coastal eutrophication from land use account for about the same amount of variation as our analogous reservoir relations (Meeuwig 1999).

About 90% of all Missouri reservoirs were constructed in the past 50 years and many are half that age. Land-use practices have not been constant over this period, but pre-impoundment land cover was undoubtedly similar to current conditions, being dominated by forest or cropland with interspersed grass. These land-use patterns would have directly influenced stream water quality (Perkins et al. 1998) and, beginning with impoundment, determined reservoir water quality. In this respect, Missouri reservoirs differ from many temperate lakes that have experienced cultural eutrophication resulting from post-settlement changes in land use (Field et al. 1996; Soranno et al. 1996). Land-cover data from a subset of the catchments ($n = 29$) that coincide with the period of our water-quality information (ca. 1980 – present) show virtually no change in the proportion of forest (a median increase of 2%) but a small decline in cropland and a concurrent increase in the proportion of grass (median changes of –8% and +12%, respectively). This shift in cover type is consistent with changes in agricultural policy over the period. The inference is that in the near term, cropland will not expand but large-scale declines in row-crop agriculture are also unlikely. Our analysis suggests that efforts to improve reservoir water quality in the state should focus on minimizing non-point nutrient sources. Research on nutrient loss from agriculture has shown that small "hot spots" often account for most nutrient export (Gburek et al. 2000) and that measures such as riparian-zone management can decrease nutrient loss (Osborne and Kovacic 1993; Soranno et al. 1996). The full potential for what are called best management practices (e.g., Mostaghimi et al. 2001) to control non-point-source nutrients has not been realized. When technological nutrient management is routinely practiced, the importance of cropland to nutrient levels in Missouri reservoirs will likely diminish.

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Acknowledgments

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Over-winter lipid depletion and mortality of age-0 rainbow trout (*Oncorhynchus mykiss*)

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Abstract: In this study we identify the size-dependent risk of winter starvation mortality as a strong selective pressure on age-0 rainbow trout (*Oncorhynchus mykiss*) that could promote the risk-taking behaviour and allocation of energy to lipids previously observed in young trout cohorts. Age-0 trout subjected to simulated winter starvation conditions gradually depleted lipid reserves to a critical minimum lipid content below which death occurred. Small fish with lower lipid content exhausted lipid reserves earlier, and experienced high mortality rates sooner, than larger fish with greater lipid content. Consequently, winter starvation endurance was dependent upon size-dependent lipid reserves and winter duration. To validate the laboratory findings in the field, we stocked several size classes of hatchery-raised trout with known lipid content at the start of winter into two experimental lakes, and estimated survival and lipid depletion at winter's end. Larger age-0 trout had greater initial lipid reserves than smaller trout. Individuals depleted most of their lipid reserves over the winter, and experienced mortality that ranged from just under 60% for the largest individuals to just over 90% of the smallest individuals. Many survivors had lipid contents near, but none were below, the minimum lipid content determined in the laboratory.

Résumé : Nous identifions dans cette étude le risque de mourir de faim pendant l'hiver, un facteur relié à la taille, chez des truites arc-en-ciel (*Oncorhynchus mykiss*) d'âge 0, comme une importante pression sélective qui pourrait favoriser des comportements de prises de risques, de même que l'allocation de l'énergie vers les lipides, ce qui a été observé antérieurement chez des cohortes de jeunes truites. Des truites d'âge 0 soumises à des conditions simulées de manque de nourriture en hiver perdent graduellement leurs réserves de lipides jusqu'à un contenu minimal critique de lipides, sous lequel la mort s'ensuit. Les petits poissons avec de faibles contenus de lipides épuisent leurs réserves de lipides et subissent de forts taux de mortalité plus tôt que les poissons plus grands avec un contenu de lipides plus élevé. En conséquence, la tolérance au manque de nourriture en hiver est reliée aux réserves de lipides qui sont fonction de la taille, ainsi qu'à la durée de l'hiver. Afin de valider ces résultats de laboratoire en nature, nous avons ensemencé au début de l'hiver des truites de pisciculture de différentes tailles ayant un contenu de lipides connu dans deux lacs expérimentaux et estimé à la fin de l'hiver la survie et la perte de lipides. Les truites d'âge 0 plus grandes ont des réserves initiales de lipides plus importantes que les truites plus petites. Les individus ont épuisé l'essentiel de leurs réserves de lipides au cours de l'hiver et subi une mortalité qui a varié de juste sous 60 % chez les plus grands à juste au-dessus de 90 % chez les plus petits. Plusieurs des survivants avaient des contenus en lipides près du minimum déterminé en laboratoire, mais aucun n'avait de valeur inférieure.

[Traduit par la Rédaction]

Introduction

Identifying constraints on prey fish behaviour is critical to our mechanistic understanding of factors affecting growth and recruitment of prey fish populations. In temperate environments, fish experience short growing seasons that precede periods of winter resource scarcity, which imposes a time constraint on acquiring energy reserves sufficient to survive winter (Schultz and Conover 1999; Post and Parkinson 2001). This time constraint can affect the trade-off between growth and mortality rates in prey, resulting in an increase in risk-taking behaviour by individuals striving to accumulate an energy insurance for the winter (Rowe and Ludwig 1991; McNamara and Houston 1994; Johansson and Rowe 1999).

If over-winter mortality is inversely proportional to accumulated energy reserves, then the risk of winter starvation operating within the constraint of a short growing season has the potential to be a strong selective pressure that could promote risk-taking behaviour (e.g., Schindler 1999; Biro et al. 2003*b*, 2003*c*) and allocation of energy to lipids in prey fish populations (Shultz and Conover 1999; Post and Parkinson

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2001). Over-winter mortality due to depletion of lipid stores is often cited as a major source of mortality for young fish populations (e.g., Bernard and Fox 1997; Hurst and Conover 1998; Pratt and Fox 2002). Studies generally show that smaller individuals experience higher mortality than larger ones. However, size-dependent depletion of energy reserves and high over-winter mortality of young fish are not universal, and may vary with the species considered, fish density, predator density, and food abundance (e.g., Garvey et al. 1998; Gotceitas et al. 1999; see review in Pratt and Fox 2002). In fact, most of the literature dealing with this issue is focused on Perciformes (e.g., Oliver et al. 1979; Toneys and Coble 1980; Post and Evans 1989) and comparatively little has been done with Salmoniformes (but see Gardiner and Geddes 1980; Simpkins et al. 2003). The most frequently invoked mechanism for size-dependent over-winter mortality is size-dependent starvation endurance. Larger fish of the same species not only tend to have greater lipid reserves than smaller individuals at the start of winter (reserves $\propto$ mass^{b}), but also have lower specific metabolic rates than smaller individuals (metabolism $\propto$ mass^{-b}; Shuter and Post 1990; Schultz and Conover 1999; Post and Parkinson 2001). Therefore, smaller individuals should experience higher winter mortality due to a combination of lower energy reserves and higher metabolism, provided they are starving.

Whole-lake experiments have shown that the presence of predatory rainbow trout (*Oncorhynchus mykiss*) elicits refuging behaviour and dramatically reduces growth and survival of age-0 rainbow trout relative to age-0 trout in lakes without them (Landry et al. 1999; Biro et al. 2003*b*). The high mortality rates of age-0 trout, which occur despite the use of refuges, are thought to result from density (Biro et al. 2003*a*) and food-dependent risk-taking (Biro et al. 2003*b*, 2003*c*) brought on by the need to accumulate lipid stores prior to winter (Post et al. 1999; Post and Parkinson 2001; Biro et al. 2003*c*). Indeed, larger age-0 trout have relatively more lipid than smaller individuals by autumn, suggesting that strong size- and lipid-dependent over-winter mortality selects for energy allocation to lipids (Post and Parkinson 2001). However, high over-winter mortality and a link to depleted lipid stores remain to be demonstrated for this species in order to identify risk of winter starvation as a major selective pressure on young fish. If there is such a link, this would support the hypothesis that predation and over-winter mortality are the two major selective forces that shape the behaviour and life history of young fish and affect their growth and survival.

In this study we show in laboratory and whole-lake experiments that over-winter mortality of young trout is high, size-dependent, and linked to the depletion of lipid reserves to a critical minimum whole-body lipid concentration. First, we quantify the size-dependent depletion of lipid reserves and mortality of age-0 rainbow trout subjected to simulated winter conditions in an outdoor greenhouse, in the absence of predators. This establishes a link between mortality and lipid depletion, and identifies lipid concentration at death. Next we validate the laboratory results by quantifying the size-dependent over-winter mortality and depletion of lipid reserves of age-0 trout stocked into two natural lakes containing fish predators. We then compare the observed size-dependent loss of lipids in these two lakes with lipid loss predicted from metabolic allometry, assuming starvation.

Methods

Laboratory experiment

We simulated winter conditions in four 450-L aquaria held in an outdoor greenhouse, where we implemented a factorial experiment using two size classes of age-0 rainbow trout and two feeding regimes. Water temperature was maintained at 3 ± 1 °C for the duration of the 100-day experiment. We obtained trout from a local hatchery, raised them under two temperature and feeding regimes to produce two size classes, and clipped the adipose fin of the larger trout to identify them. We stocked each tank with 200 large trout (mean fork length (FL) = 40 mm, mean mass = 0.75 g, standard error (SE) = 0.04 g, n = 35) and 165 small trout (mean FL = 31 mm, mean mass = 0.41 g, SE = 0.019 g, n = 35). There were no differences among replicate tanks in the initial lengths of large or small trout ($F < 1$ and $P > 0.05$ in each case). At this time, a random subsample of 30 large and 30 small fish were frozen for subsequent lipid analysis. Each tank and common filter boxes were equipped with airstones to allow adequate circulation and oxygen. Each tank had a Styrofoam™ cover on the water surface that simulated ice cover but still allowed fish to experience a natural winter photoperiod. Two tanks were randomly allocated to the feeding treatment, in which fish were fed ad libitum daily, and remaining replicate fish cohorts went unfed for the duration of the experiment. Any dead fish were collected each day and frozen for lipid analysis. In addition, we sampled seven large and seven small trout from each replicate every 30 days to monitor changes in lipid concentration of survivors over time.

To obtain sufficient material for lipid analysis, trout were pooled into groups of seven. Thus, lipid concentration of dead fish was represented by a seven-fish aggregate sample collected over 1–7 days, where the midpoint date of the period over which individuals were collected was taken as the date of death for each aggregate sample. Fish were thawed, weighed, measured for length, and dried at 50 °C for 96 h. The dry samples were reweighed and then ground with mortar and pestle. Lipids were extracted using the methanol and chloroform procedure of Folch et al. (1957) and adopted by Post and Parkinson (2001). This method involves measuring 0.3–0.5 g (measured to within ±0.0001 g) of finely ground sample into a test tube, adding 16 mL of a 50:50 methanol:chloroform solution, and then heating the mixture to a boil in a water bath set at 61 °C. The mixture is then cooled to room temperature and chloroform added to bring the volume up to 25 mL. This solution is then filtered through a No. 1 Whatman filter paper into a separatory funnel. Next, 10 mL of 0.9% saline solution is added to the funnel to remove impurities from the mixture. This leaves pure lipid in the methanol–chloroform layer that settles to the bottom of the funnel. This bottom layer is drained into a preweighed beaker and evaporated to dryness on a hot plate at 70 °C (Post and Parkinson 2001). The mass of the remaining lipid in the beaker represents the mass of lipid contained in the dry fish sample. We calculated mean lipid-depletion rates for small

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and large trout from the difference between individual lipid concentrations at death and the mean lipid concentration for the cohort at the start of the experiment.

Field experiment

Our two lakes are located within 20 m of one another in south-central British Columbia, Canada (49°50′N–49°56′N, 120°33′W–120°34′W). The lakes lack naturally reproducing fish populations, are 2.0 and 3.2 ha, and are relatively shallow (maximum depths 9–14 m). The littoral habitat in the lakes consists of aquatic macrophytes (primarily *Chara* sp. and *Myriophyllum* sp.) located in small patches, open sediment, gravel, rocks, woody debris, and fallen trees. The lakes are best described as mesotrophic, based upon phosphorus concentrations (Biro et al. 2003*c*).

Rainbow trout for the field experiment were raised from eggs collected from wild populations in Tunkwa Lake at the Fraser Valley Trout Hatchery (B.C. Fisheries Branch). The trout were sorted into four non-overlapping size classes based on fork length (and uniquely marked with fin clips) that ranged from 50 to 105 mm (for the four size classes: mean FL = 61, 69, 78, and 89 mm; standard deviation (SD) = 0.3, 0.2, 0.2, and 0.5 mm; n = 50 for each). Lakes K1 and K2 each received 400 of each size class on 17 November 2000 after the fish were chilled from 12 °C down to 3 °C during the 4-h transit from the hatchery. Two centimetres of ice were present on the lakes on the day of stocking, indicating they had frozen over recently. After stocking into shallow water, the fish were clearly visible beneath the ice; they appeared to be in good condition, and no losses of fish were observed.

Spring gillnet sampling was used to estimate survival of age-0 trout over the winter. Gillnetting took place over a 5-day period in lakes K1 and K2, beginning on 23 April 2001, when the ice cover had receded at least 10 m from the shoreline; all ice had melted before the last day of netting. Sinking experimental gillnets were set for 5 consecutive nights in all habitats, and comprised graded mesh sizes ranging from 13 to 50 mm (stretched mesh). Gillnet densities were standardized among lakes on an area basis and ranged from 400 to 500 $m^2 \cdot ha^{-1} \cdot night^{-1}$, following the identical netting effort and protocol used previously in these lakes (Post et al. 1999; Biro et al. 2003*b*). Mortality and growth over the winter were estimated by adjusting the total 5-night catch of age-0 trout of a given length by an established size-specific vulnerability function determined from previous mark–recapture experiments in the lakes (for details see Biro et al. 2003*b*). The gillnets caught trout >45 mm FL, which is well within the minimum size of the stocked trout. We did not use mesh sizes larger than 50 mm, to prevent killing adult trout from the recreational fishery. Consequently, we do not have a direct estimate of potential predator density during the winter. However, lakes K1 and K2 are stocked with yearling trout every spring at 250 and 180 trout·ha^{-1}, respectively.

Several hundred captured trout from each lake were frozen for lipid analysis. Random samples, stratified by length, of the frozen age-0 trout were selected from each lake for regression analyses. The stratified samples included the full range of body sizes of fish captured in our gillnets. To infer the extent of over-winter lipid loss in the field experiment, we compared the observed allometry of lipid loss to the loss of lipids that is predicted from metabolic allometry assuming starving fish. We used the metabolic slope coefficient for rainbow trout (Rand et al. 1993), and our estimates of mean lipid loss rates for our two sizes of trout used in the laboratory experiment, to fit the intercept of the relationship by least-squares. We applied this predicted mass-dependent rate of lipid loss to the autumn lipid concentrations of the hatchery fish, and the observed winter duration, to obtain a predicted loss of lipids over the winter. In addition, we used the observed allometry of autumn lipid concentration, and mean lipid concentration at death, to calculate the proportion of lipids that could be lost before death.

Statistical analysis

We used maximum-likelihood techniques, rather than less powerful traditional parametric statistics, on mortality data from the two field experiments because each datum (replicate) represents the response in a single lake. Significance in this analysis was determined using Type III likelihood-ratio tests that are asymptotically χ^2 distributed with df = 1 (Burnham and Anderson 1998). Thus, a likelihood-ratio test with $P < 0.05$ indicates a statistical model that is significantly more likely than a null model in which the response is constant (i.e., slope estimate not different from zero). All remaining analyses used standard linear regression or analysis of covariance. Age-0 trout mortality data were analyzed assuming normally distributed errors on arcsine square-root transformed data. We arcsine square root transformed all dependent variables that were expressed as a proportion to satisfy normality assumptions, and $\log_{10}$-transformed fish length and mass to satisfy linearity assumptions. To ensure statistical independence in the regression analyses of lipid allometries, we used length rather than mass as the predictor variable.

Results

Laboratory experiment

Starved age-0 trout lost substantial lipids and experienced high mortality (Fig. 1*a*). Lipid concentrations at the time of death were similar for small and large trout that were starved (0.0099 and 0.0081 g lipid·g^{-1} wet mass, respectively, suggesting a minimum lipid threshold for survival (Fig. 1*a*). Lipid concentration at death was related to trout size ($F_{[1,38]} = 9.3$, $P < 0.005$) but not to time of death or to the interaction between time and fish size ($P > 0.5$ in both cases; Fig. 1*a*). Smaller trout began dying earlier than larger trout, the timing of their death being related to the decline in lipid content of survivors to near the average lipid content at death (Fig. 1*a*). High mortality rates began later for larger trout because they had relatively more lipid at the outset (Fig. 1*a*). Clearly, high mortality rates for trout with low lipid stores (at approximately 30 days for small trout and 80 days for large trout) resulted in upwardly biasing lipid estimates of survivors at 60 days for smaller trout and 90 days for larger trout (Fig. 1*a*). Small starved trout had all died before the end of the experiment, owing to their lower lipid content at the start of winter, and slightly higher minimum lipid threshold (Fig. 1*a*). In contrast to our expectations, the estimated

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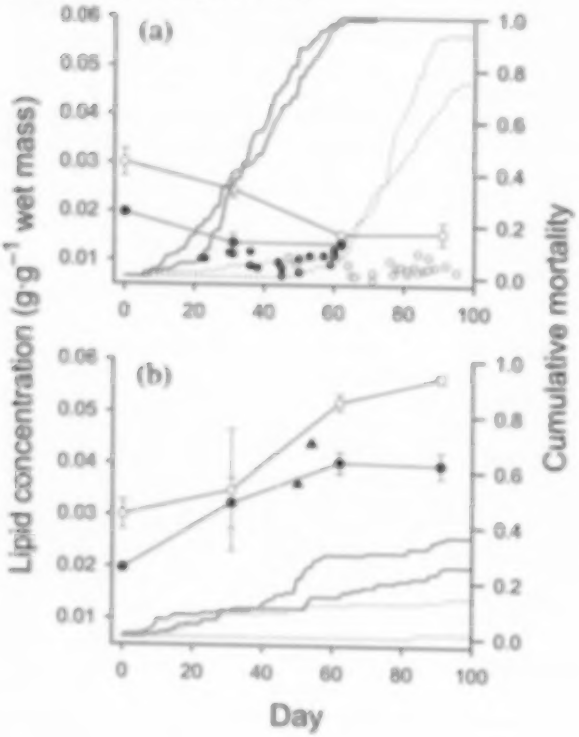
Fig. 1. Lipid concentrations and cumulative mortality of two size classes of age-0 rainbow trout (*Oncorhynchus mykiss*) experiencing winter conditions in a outdoor greenhouse under starvation (*a*) and fed to satiation (*b*). Mean lipid concentrations (± standard error) of survivors over time and mortality trajectories for each replicate tank are shown. Individual data points represent lipid concentration of age-0 trout at the time of their death. Solid lines and symbols represent the small size class; dotted lines and open symbols represent the large size class. The solid triangles in *b* represent lipid concentration at death for fed fish that had died as a result of fungal infection.



mean rate of lipid depletion was lower for small trout than for large trout (0.000 244 6 and 0.000 296 2 g lipid·g wet mass^{-1}·day^{-1}, respectively).

By contrast, lipid concentration increased over time when trout were fed ad libitum, and their mortality was low (Fig. 1*b*). Mortality was attributed to fungal infections in all cases, and the lipid concentration of dead fish was similar to that of survivors. As expected, larger fed trout accumulated more lipid than smaller fed trout (Fig. 1*b*).

Field experiment

Over-winter mortality of age-0 trout was high and size-dependent (Fig. 2*a*). Smaller age-0 trout experienced greater over-winter mortality than did larger trout (R^2 = 0.86; likelihood-ratio test: χ^2 = 15.8, $P < 0.0001$). Trout from lake K2 experienced lower mortality than fish from lake K1 (lake effect: χ^2 = 4.9, $P < 0.03$; R^2 = 0.92, for the combined size and lake effects; Fig. 2*a*), but there was no interaction effect between fish size and lake origin ($P > 0.1$). The mean mass of survivors was 5.99 g in lake K1 and 7.26 g in lake K2. These differences in mean mass must to some extent reflect over-winter growth rates given that maximum fish lengths were greater in spring than in autumn (Figs. 2*b* and 2*c*), and the mean mass of these cohorts was only 4.4 g in autumn (n = 400). Total over-winter mortality of age-0 trout cohorts in lakes K1 and K2 was 73% and 67%, respectively.

At the start of winter, larger age-0 trout had greater lipid mass than did smaller trout ($F_{[1,28]}$ = 531, $P < 0.0001$, R^2 = 0.95; Fig. 2*b*). By spring, age-0 trout had significantly depleted lipid stores (season effect: $F_{[1,84]}$ = 215, $P < 0.0001$), but there was no interaction between season and fork length ($F_{[1,84]}$ = 0.09, $P > 0.7$). Parallel lipid allometries on log–log-transformed data indicate that larger fish actually lost more lipid than did smaller fish, contrary to our expectations (Fig. 2*b*). Spring samples of age-0 trout from lake K2 had significantly greater lipid mass at a given length than fish from lake K1 (lake effect: $F_{[1,54]}$ = 16, $P < 0.0002$) but the slopes did not differ (interaction effect: $F_{[1,54]}$ = 0.01, $P > 0.9$). There was greater between-individual variation in lipid stores at a given length for fish captured in the spring than at the start of winter (K1: R^2 = 0.87; K2: R^2 = 0.79, $P < 0.0001$ in each case).

At the start of winter, larger age-0 trout had higher lipid concentrations than did smaller trout ($F_{[1,28]}$ = 68, $P < 0.0001$, R^2 = 0.71; Fig. 2*c*). Age-0 trout had significantly lower lipid concentrations at the end of the winter (season effect: $F_{[1,84]}$ = 252, $P < 0.0001$) but there was no interaction between season and fork length ($F_{[1,84]}$ = 1.52, $P > 0.2$). Again, parallel relationships on this nonlinear scale indicate that larger fish lost a greater proportion of accumulated lipids than did smaller fish. Spring samples of age-0 trout from lake K2 had higher lipid concentrations, at a given length, than fish from lake K1 (lake effect: $F_{[1,54]}$ = 16, $P < 0.0002$), but the slopes did not differ (interaction effect: $F_{[1,54]}$ = 0.7, $P > 0.4$). As before, there was greater inter-individual variation in lipid concentration for fish captured in the spring than for those captured at the start of winter (K1: R^2 = 0.43; K2: R^2 = 0.33, $P < 0.002$ in each case).

Although larger fish lost absolutely more lipids than smaller fish over winter (Fig. 2*b*), the proportion of lipids lost over the course of the winter was between 60% and 80% of their lipid stores, which is near the maximum (approximately 85%) that they could afford to lose before starving to death (Fig. 3). In addition, there was little difference in lipid consumption between small and large fish (Fig. 3). This observation contrasts dramatically with the rapid nonlinear decline in the proportion of lipids lost that is predicted by size-dependent metabolic rates for starving fish (Fig. 3). Consequently, the metabolic allometry prediction correctly predicted lipid loss of the smallest fish but greatly underestimated lipid loss for the larger fish (Fig. 3). Survivors of all sizes lost much of their available lipids (that in excess of the minimum lipid concentration), bringing many individuals near death by starvation (Figs. 2*c* and 3).

Discussion

Our study sought to determine if over-winter mortality of age-0 trout is high and inversely proportional to accumulated body reserves, as expected for starving individuals. If so, then over-winter mortality is a strong selective force that

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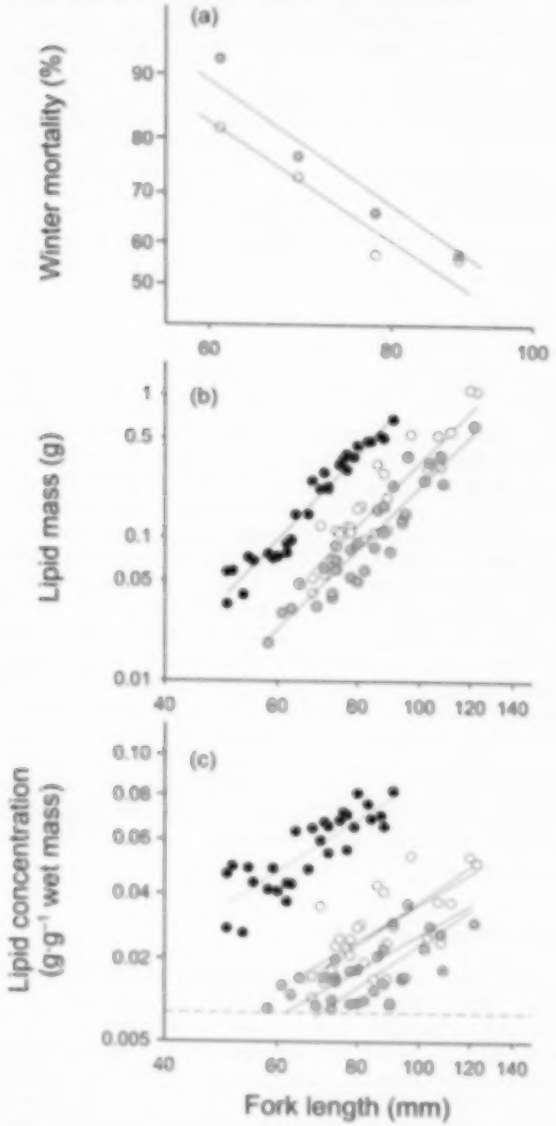
Fig. 2. (*a*) Mortality of age-0 rainbow trout as a function of mean autumn fork length in two replicate lakes. (*b*) Allometry of lipid mass for age-0 trout in autumn and spring in two replicate lakes. (*c*) Allometry of lipid concentration in autumn (solid symbols) and spring in two replicate lakes. Open and shaded symbols represent estimates in lakes K2 and K1, respectively. The broken line represents the mean lipid concentration at death for starving trout determined in the laboratory experiment.



could promote density- and food-dependent risk-taking behaviour (Biro et al. 2003*a*, 2003*b*, 2003*c*) and allocation of energy to lipids observed for age-0 trout cohorts (Post and Parkinson 2001; this study). Together, the results of the laboratory and whole-lake experiments indicate that the risk of winter starvation is high and size-dependent, and is related to the loss of lipids to a threshold minimum lipid concentration. Therefore, the risk of winter starvation is a strong selective pressure that can promote risk-taking and lipid accumulation in populations of age-0 trout. In a more general sense, identifying predation (Biro et al. 2003*b*, 2003*c*) and over-winter starvation risks (this study) as major selective pressures for young fish may explain, at least in part, the high mortality rates typically observed for young fish populations during the growing season.

In the laboratory, age-0 trout gradually depleted lipid reserves over time and died when they reached a critical minimum lipid concentration of just less than 1% of total wet mass. The onset of high mortality rates coincided with the depletion of lipid reserves to levels near this critical lipid concentration, at which the first fish to die were those with the lowest lipid reserves at the outset. Larger trout, with more lipid reserves, began to die 40 days later than the small size class of trout with less lipid reserves. In the field, a similar pattern emerged in which smaller fish with fewer lipid reserves experienced greater mortality than larger trout with more lipid. The observation that no individuals were observed with less than 1% lipid in the spring suggests that this critical minimum lipid concentration needed for survival is robust, and the actual value does apply to fish of a much larger size range than that used in the laboratory experiment. In other studies, evidence has also been found for minimum lipid content thresholds for survival in fishes (see Post and Parkinson 2001), but to our knowledge our study is the first to convincingly demonstrate a minimum lipid threshold, and high over-winter mortality, in controlled laboratory and field experiments for a salmonid species. However, Simpkins et al. (2003) also found evidence for a threshold minimum lipid content for rainbow trout in the laboratory. Unfortunately, direct comparison is difficult, as they report the critical concentration of 3.2 as a percentage of dry mass (Simpkins et al. 2003), and wet mass to dry mass ratios are not constant among individuals or groups.

The smallest individuals in our field experiment appeared to lose lipids at a rate that was consistent with standard metabolic allometry of inactive, starving fish. Our predictions indicated that fish less than 50 mm FL would die over the course of the observed 150-day winter. Indeed, we observed only one individual less than 60 mm FL by spring in the lakes. To our surprise, however, larger individuals consumed more of their lipid reserves than predicted by standard metabolic allometry. Greater lipid consumption suggests higher energy costs for larger fish, perhaps because of increased activity rates associated with competitive and (or) predatory interactions with other trout. It is difficult to assess whether fish died directly from starvation per se, or were eaten by larger trout as they neared starvation in poor condition. However, it is possible that potential cannibals may increase starvation mortality of young trout by increasing activity levels through predator avoidance. This would result in smaller individuals being eaten or starving to a greater extent than larger ones, and could explain the 60% mortality observed for the largest size class (90 mm FL) that are not likely to be consumed by adult rainbow trout (Johnsson 1993; Biro et al. 2003*b*).

Mortality of age-0 trout declined dramatically with increases in body size, with trout of 60 mm FL or less experiencing at least 90% mortality and those of 90 mm FL only 60%. Clearly, this indicates that winter food shortage and

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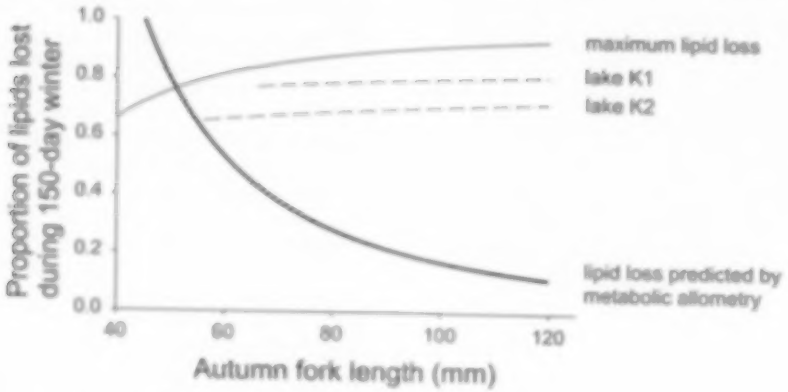
Fig. 3. Proportion of lipid stores lost over the 150-day winter in relation to fish mass at the onset of winter. The thin solid line represents the proportion of lipid reserves that could be consumed before death by starvation, based on a minimum lipid content of 0.9% determined in the laboratory. The thick solid line represents the loss of lipids predicted from metabolic allometry, assuming inactivity and starvation. The broken lines represents the observed loss of lipids over the winter in our two experimental populations calculated by subtracting autumn and spring lipid allometries in Fig. 2, in which the length of each broken line represents the range of body sizes of fish surviving to the end of the winter.



starvation may be a major mechanism of population regulation for age-0 trout, which amplifies the strong density- and food-dependent mortality they experience during the growing season. For instance, growing-season mortality of age-0 trout ranges from as little as 55% to as much as 98%, and is related to density- and food-dependent individual risk-taking behaviour (Post et al. 1999; Biro et al. 2003*a*, 2003*c*). Mean autumn mass, and therefore mean lipid content, of age-0 trout also declines with increases in density and (or) reductions in food abundance (Post and Parkinson 2001; Biro et al. 2003*a*, 2003*c*) that would, in turn, reduce over-winter survival. If, for instance, age-0 trout experienced 90% mortality during the growing season, and reached a population mean body size that would result in 70% over-winter mortality (as in our field experiment), then only 3% of the cohort would remain alive as age-1 individuals the following growing season. Such a pattern of fish mortality may be common for age-0 fishes in temperate waters. For instance, recruitment of age-1 striped bass (*Morone saxatilis*) was better predicted by the winter duration than by indices of age-0 abundance in one field study (Hurst and Conover 1998). The magnitude of over-winter mortality that we observed in the field is likely an underestimate of the mortality of trout reared naturally in lakes, owing to greater lipid content in our hatchery-reared trout. Indeed, the hatchery-raised fish had a lipid allometry with the same slope as that observed for fish reared naturally in lakes, but with a significantly higher intercept, indicating greater lipid stores at a given length (hatchery fish: $\log_{10}$ lipid mass = –4.76 + 4.81(FL), 95% confidence interval (CI) = –5.1 to –4.4 and 4.4–5.3 for the intercept and slope, respectively; naturally reared fish: $\log_{10}$ lipid mass = –5.2 + 5.1(FL); Post and Parkinson 2001).

Starvation of young trout was clearly not the result of an inability to feed or metabolize food at low temperatures. Age-0 trout increased lipid reserves during winter when they were provided with food ad libitum in the greenhouse experiment, and there was evidence that fish also did grow to a small extent in the field. Small and large trout nearly doubled their lipid concentration over the 100-day winter when fed, indicating that young rainbow trout can perform quite well at these low temperatures when provided with abundant prey. Therefore, the combined results from both experiments indicate that winter prey is rare in lakes, given that the nonfeeding treatment in the greenhouse provided food conditions much closer to those experienced by fish in the field than did the ad libitum treatment in the greenhouse. We speculate that the reason why the age-0 trout were able to grow to a small extent in the field, yet consume most of their lipid reserves, was a greater availability of food early in the winter, which allowed some growth, followed by food shortage during the remainder of the winter. Future studies might examine lipid depletion and mortality of a greater size range of young trout to develop a functional relationship for size- and lipid-dependent probability of mortality. In addition, examining the costs and benefits to young fish adopting different energy-allocation strategies, and the short- and long-term mortality consequences of those strategies, would shed light on the patterns of behaviour and energy allocation we see in young fish populations.

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Hydrogen peroxide distribution, production, and decay in boreal lakes

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Abstract: The distribution, production, and decay of hydrogen peroxide (H_2O_2) were studied in 10 boreal lakes of differing physical–chemical characteristics. Diurnal and vertical fluctuations in H_2O_2 concentration were followed in the lakes by sampling at six depths three times per day. In addition, incubations of water filtered through 0.2-µm mesh were made under artificial irradiation to study the abiotic production and decay of H_2O_2. H_2O_2 concentrations after 8 h of artificial irradiation were significantly correlated with neither absorption coefficients at 320 nm nor with dissolved organic carbon (DOC) concentrations. However, H_2O_2 concentration increased rapidly with DOC concentration among lakes with DOC concentrations below 10 mg·L^{-1}. The H_2O_2 concentration after exposure to ultraviolet radiation was positively related to the half-life of H_2O_2, which in turn was negatively correlated with iron and manganese concentrations (r^2 = 0.68 and 0.70, respectively). In situ H_2O_2 concentrations at the surface of the water column ranged between 30 and 1041 nmol·L^{-1} and were largely determined by the decay rates of H_2O_2 and the mixing depth of the water column.

Résumé : Nous avons étudié la répartition, la production et la décomposition du peroxyde d'hydrogène (H_2O_2) dans 10 lacs de la région boréale qui possèdent des caractéristiques physicochimiques différentes. Nous avons fait des prélèvements à six profondeurs, trois fois par jour, dans les lacs afin de suivre les fluctuations journalières et verticales des concentrations d'H_2O_2. De plus, nous avons incubé de l'eau filtrée sur un filtre de 0,2 µm sous irradiation artificielle afin d'observer la production et la décomposition abiotiques d'H_2O_2. Après 8 h d'incubation sous irradiation artificielle, il n'y a pas de corrélation significative entre les concentrations d'H_2O_2 et les coefficients d'absorption à 320 nm, ni entre ces concentrations et le carbone organique dissous (DOC). Cependant, les concentrations d'H_2O_2 augmentent rapidement en fonction de DOC dans les lacs qui ont des concentrations de DOC inférieures à 10 mg·L^{-1}. Après une exposition à le rayonnement ultraviolet, la concentration d'H_2O_2 est en corrélation positive avec la demi-vie d'H_2O_2, qui, à son tour, est en corrélation négative avec le fer et manganèse (r^2 = 0,68 et 0,70, respectivement). Les concentrations d'H_2O_2 in situ en surface de la colonne d'eau varient de 30 à 1041 nmol·L^{-1} et s'expliquent en grande partie par les taux de décomposition d'H_2O_2 et la profondeur du brassage dans la colonne d'eau.

[Traduit par la Rédaction]

Introduction

The interaction between ultraviolet (UV) radiation and dissolved organic carbon (DOC) can result in the formation of chemically reactive and biologically toxic compounds, including hydroxyl- and alkyl-peroxyl radicals (Mill et al. 1980), superoxides, and hydrogen peroxide (H_2O_2) (Cooper et al. 1988). H_2O_2 is long-lived compared with other oxidants and radicals and is measurable by simple methods, making it a useful marker of DOC photolysis and of the photochemical production of oxidizing agents (Cooper et al. 1989*b*). Diel patterns of H_2O_2 concentration in surface waters have been observed in several studies, with higher concentrations during the day and lower during the night (Cooper et al. 1989*a*; Herrmann 1996; Wilson et al. 2000*a*). This pattern suggests that photochemical formation is the major production mechanism of H_2O_2 in fresh waters and seawater (Cooper and Zepp 1990). In addition, biological (Wilson et al. 2000*b*) and trace metal mediated production in darkness (Moffett and Zika 1987), as well as wet and dry deposition (Miller and Kester 1994), can contribute to the H_2O_2 concentration in natural waters.

Typical H_2O_2 concentrations between 10 and 400 nmol·L^{-1} at the surface have been reported in a number of different types of aquatic ecosystems (Cooper et al. 1989*a*; Kieber and Helz 1995; Herrmann 1996). H_2O_2 concentrations up to 800 nmol·L^{-1} in lakes have also been observed (Cooper and Lean 1989), a level that is inhibitory to bacteria (Xenopoulos and Bird 1997). In most cases, H_2O_2 concentrations are higher in fresh waters than in the sea, while estuarine re-

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Table 1. Description of the lakes in this study.

Lake	Location[a]	DOC concn. ($mg \cdot L^{-1}$)[b]	pH	Iron concn. ($\mu g \cdot L^{-1}$)[c]	Manganese concn. ($\mu g \cdot L^{-1}$)[c]	UV-A ($kJ \cdot m^{-2}$)[d]	Absorptivity at 320 $nm \cdot m^{-1}$
Klintsjön	57°08′, 14°42′	3.1	5.3	44	59.7	524	6.0
Skärlen	57°11′, 14°52′	3.6	6.0	2.5	2.9	492	5.6
Hindsen	57°13′, 14°09′	5.0	7.2	8.2	1.3	575	12.2
Övingen	57°14′, 14°43′	6.8	6.9	13	1.2	301	15.7
Homeshultasjön	57°13′, 14°50′	9.5	7.2	41	1.1	557	27.7
Stråken	57°07′, 14°34′	11.6	6.7	441	13.7	482	46.3
Stavsjön	56°38′, 13°36′	11.9	4.2	230	6.5	240	72.1
Älgarydssjön	57°11′, 14°17′	12.4	5.3	1110	6.4	553	61.2
Skärshultsjön	57°09′, 14°31′	17.2	6.1	983	81.4	408	87.9
Grunnen	57°10′, 14°26′	19.4	7.2	1080	15.3	487	107.7

[a]Geographic coordinates are given as latitude (N) and longitude (E).
[b]Dissolved organic carbon.
[c]Total concentration.
[d]Integrated amount of ultraviolet-A radiation at the surface during the incubations in each lake, between 0900 and 1700.

gions exhibit intermediate values (Kieber and Helz 1995). A positive relationship between DOC and H_2O_2-formation rates has been detected in previous studies (Cooper et al. 1988; Scully et al. 1996), which may partially explain the difference in H_2O_2 concentrations between freshwater and marine systems.

The decay of H_2O_2 is influenced by both biotic and abiotic factors and varies widely among different aquatic ecosystems. The decay of H_2O_2 may be affected by bacteria (Cooper and Zepp 1990) and other microorganisms (Cooper and Lean 1989), and by redox-sensitive metals such as iron (Moffett and Zafiriou 1993) and manganese (Sunda and Huntsman 1994). The possibility has often been raised that biological decay is the main mechanism of H_2O_2 decay, at least in coastal and marine surface waters (Moffett and Zafiriou 1990). Only a few studies in which H_2O_2 decay was considered have been conducted in metal- or DOC-rich waters (Tranvik and Kokalj 1998; Wilson et al. 2000*b*). Humic lakes are usually distinguished by the presence of high amounts of metals, which can be reduced by H_2O_2. Sunda and Huntsman (1994) found an approximately fivefold decrease in the rates of manganese dissolution after addition of H_2O_2 catalase during light exposure of simulated estuarine water. The results found by Sunda and Huntsman (1994) suggest that photodissolution of manganese oxides results mainly from manganese reduction by H_2O_2. Evidence from the literature also shows that H_2O_2 is involved in both reduction (King et al. 1993) and oxidation of iron (Moffett and Zika 1987).

The aim of this study was to determine the distribution, production, and decay of H_2O_2 in boreal lakes of differing physical–chemical characteristics. In situ measurements were undertaken to study the diurnal and depth distribution of H_2O_2. There are only few studies linking the factors that influence production and decay of H_2O_2 under laboratory conditions and the distribution of H_2O_2 in natural conditions. The main objective of this study was to emphasize the role of metals in the distribution of H_2O_2 in humic lakes, as most of the previous studies were conducted in seawater and clear-water lakes. Differences in DOC and metal concentrations among the lakes were hypothesized to influence patterns of H_2O_2 production and decay, thus providing a better explanation of H_2O_2 dynamics in fresh waters.

Material and methods

Sampling locations

Between 19 June and 7 July 2001, in situ H_2O_2 concentrations were measured in 10 oligotrophic lakes situated within the boreal region of the South Swedish Highlands. Chlorophyll *a* and phosphorus concentrations in these lakes range between 3–12 and 1–14 $\mu g \cdot L^{-1}$, respectively (data not shown). The locations of lakes and their physical–chemical characteristics are presented in Table 1.

Diurnal and vertical fluctuations in H_2O_2 concentration

Diurnal and vertical fluctuations in H_2O_2 concentration were followed in one lake per day by sampling at six depths (i.e., surface and 0.5, 1.0, 1.5, 2.0, and 3.0 m) in the euphotic zone of the water column three times per day (0930, 1230, and 1530). The temperature at each sampling depth was also measured. Approximately 40-mL samples were collected from each depth in acid- (10% HCl) and Milli-Q-rinsed glass bottles. Thereafter, triplicate 3-mL samples were added to 6-mL vials containing 90 µL of *N*-acetyl-3,7-dihydroxyphenoxanine (APOXA) working solution (see below). The vials were placed in a rack on ice clamps covering the bottom of a cooling box. All samples were analyzed the same evening, and maximum storage time before analysis was approximately 10 h.

Measurements of H_2O_2 production under in situ conditions

Incubations at the water surface were performed in each lake to measure H_2O_2 production under sterile conditions. A water sample was taken from the epilimnion of each lake, using a 2 m long Plexiglas® tube. Approximately 20 L of water each was emptied into an acid- and a Milli-Q-rinsed polycarbonate bottle. Sampling in a lake was done the day before the incubation in that lake. The same day as the sampling was done, the contents of the 20-L polycarbonate bottle were filtered through a Milli-Q-rinsed GF/A filter

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(147 mm, Gelman Sciences, Montréal, Quebec) and subsequently through a 0.2 µm mesh membrane filter (147 mm, Gelman Sciences). The filtered water was put into a 10-L glass bottle, which was then stored in a refrigerator until the in situ incubation the following day. Water from the 10-L glass bottle was distributed to quadruplicate quartz tubes (inner diameter 40 mm, length 200 mm, and volume 190 mL). The tubes were suspended horizontally at the surface of the lake, with half of the tube above the water and half under the water. Quadruplicate tubes wrapped in aluminum foil were used as dark controls. The tubes were fixed horizontally on a steel-wire platform suspended from a wooden frame. All glassware used was previously acid- (10% HCl) and Milli-Q-rinsed.

The daily variation in solar radiation was estimated by measuring the integrated amounts of UV-A radiation (315–400 nm) between 0900 and 1600, using an IL 1400A radiometer (International Light Inc., Newburyport, Massachusetts, USA). In addition, downwelling radiation was measured in all lakes at 380 nm using a PUV-500 radiometer. The depth of 1% surface irradiance for radiation at 380 nm ($z1\%_{380\ nm}$) was calculated according to Kirk (1994). We chose 380 nm for calculating 1% surface irradiance because substantial H_2O_2 formation can still occur at this wavelength (Scully et al. 1996). Temperature profiles were also recorded with the PUV-500 radiometer during the sampling of water for H_2O_2 measurements (i.e., at 0930, 1230, and 1530). The depth of the epilimnion was determined on the basis of changes in temperature relative to depth (i.e., changes in temperature ≥1.5 °C·m^{-1} were regarded as the boundary for a thermocline).

Measurements of H_2O_2 production and decay in laboratory conditions

An additional 10-L integrated sample (from 0–2 m depth) was taken during the field studies and stored at 4 °C in the dark for further laboratory measurements of H_2O_2 production and decay under light- and temperature-controlled conditions. Incubations under laboratory conditions were completed approximately 2 months after the in situ sampling and incubations. Approximately 200 mL of lake water from the 10-L polycarbonate bottles was filtered through 0.2-µm-mesh filters. Thereafter, triplicate 25-mL samples were distributed into quartz tubes (40 mL volume). The tubes were irradiated for 8 h under an artificial UV radiation source consisting of eight fluorescent tubes (UVA-340, Q-Panel Company, Cleveland, Ohio, USA) emitting UV-A (15.0 W·m^{-2}), UV-B (0.37 W·m^{-2}), and photosynthetically active radiation (PAR; 5.17 W·m^{-2}). Average irradiation values for the incubations in the field at noon on a cloudless day were 24.1, 0.33, and 365 W·m^{-2} for UV-A, UV-B, and PAR, respectively, at the surface of the water column. The integrated amount of UV-A radiation received externally by the tubes during the artificial irradiation was 432 kJ·m^{-2} (average incubation in the field was 489 kJ UV-A·m^{-2}). Triplicate tubes wrapped in aluminum foil were used as controls. Immediately after incubation, the tubes were kept in the dark and H_2O_2 was measured 3, 7, 13, 26, and 51 h after irradiation was terminated. Half-lives were calculated from equations fitted (r^2 values ≥0.75) to ≥3 H_2O_2 measurement points. Asymptotic decay phases were not included in these calculations. The temperature in the room was kept constant at 18 °C during the whole experiment.

H_2O_2 measurements

H_2O_2 concentrations were derived from the enzyme-catalyzed reaction between APOXA and H_2O_2 to form a fluorescent product. Chemicals used during the study were obtained from Sigma Chemicals and used as received. APOXA and enzyme (horseradish peroxidase, Sigma Type VI, 50 units·mL^{-1}) stock and working solutions were prepared as described by Tranvik and Kokalj (1998). Briefly, 1.0 mg of APOXA dissolved in 1 mL of dimethyl sulphoxide (DMSO) was used as the stock solution. Working solutions were prepared by mixing 25 µL of the APOXA stock solution, 1 mL of Milli-Q water, and 2 mL of horseradish peroxidase. A volume of 90 µL of the working solution was added to a 3-mL sample in a 10-mL acid- (10% HCl) and Milli-Q-rinsed polypropylene vial. Depending on the time of sampling, fluorescence was measured after 1–10 h of cold storage on a Shimadzu RF-1501 spectrofluorometer with excitation and emission wavelengths of 570 and 585 nm, respectively.

Owing to the possibility of dissolved organic matter affecting the calibration slopes of H_2O_2 measurements (Miller and Kester 1988), individual calibrations were performed for each lake studied. H_2O_2 volumes of 20–50 µL, serially diluted from a stock solution, were added to triplicate 3-mL samples to achieve seven standard solutions ranging from 64 to 796 nmol·L^{-1}. Higher concentrations were analyzed by diluting the photoreacted sample with 0.2-µm-mesh filtered lake-specific water. The stock-solution concentration was determined and calibrated (molar absorptivity 38.1 mol·cm^{-1}) (Miller and Kester 1988) from absorbance at 240 nm, measured on a Beckman DU 650 spectrophotometer. Linear regression between standard H_2O_2 concentration and fluorescence for the different lakes presented slopes that ranged between 0.65 and 0.91 (all r^2 values ≥0.99), depending on the lake water. A maximal error in calculated H_2O_2 concentrations of a factor of 1.6 could have resulted if we had used a single calibration curve for all studied lakes. This variation is considerably lower than the fourfold variation in calibration slopes noted for the *p*-hydroxyphenyl-acetic acid (POHPAA) method used to measure H_2O_2 in seawater (Miller and Kester 1988). APOXA exhibits fluorescence at wavelengths in the red region (approximately 580 nm), where interfering fluorescence from dissolved organic matter is low. Analysis of freshwater samples is thus less problematic with APOXA because of lower background fluorescence (Lars Tranvik, Department of Limnology, Uppsala University, SE-752 36 Uppsala, Sweden, personal communication) compared with POHPAA, which exhibits fluorescence at approximately 350 nm (Miller and Kester 1988). However, although we detected a relatively small slope variation, calibrations are recommended for every type of lake studied. Blanks were obtained through a simplified version of the method used by Miller and Kester (1988). In contrast to their method, catalase was not added to degrade H_2O_2, since it did not affect the blank values of the samples.

Indications of temporal instability of sample fluorescence during field transport have previously been observed (Miller

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and Kester 1988). During the field measurements, the APOXA solution was added to the samples in the field, which were stored cool until further analysis in the laboratory. Storage time ranged from 4 to 10 h. Therefore, we performed a stability test, covering the specific conditions present when the H_2O_2 measurements were done in the field. H_2O_2 was added to samples from each lake and to a Milli-Q sample used as a control, to a concentration of 322 nmol·L^{-1}. Samples were then stored as during field sampling. Fluorescence reading was followed by analyzing each sample five times over a 10-h period (i.e., the maximum amount of time between sampling and reading of fluorescence). We found a linear increase in fluorescence in all types of lakes as a function of storage time (all r^2 values ≥0.95). The apparent increases in H_2O_2 concentration with storage time ranged between 4.3% and 37.3% for 10 h of storage in the cooling box (4–10 °C), and were positively related to DOC concentration ($r^2 = 0.51$, $p < 0.05$). The Milli-Q control was stable for a period of 10 h (–0.02% change in fluorescence between initial reading and after 10 h storage). The magnitude of the increase in fluorescence in the clear-water lakes due to storage during our field measurements was comparable to the changes noted for the POHPAA reagent when used for H_2O_2 measurements in seawater (Miller and Kester 1988). The temporal increase in fluorescence due to storage that seems to prevail regardless of method or system studied should be considered when samples cannot be analyzed immediately. H_2O_2 concentrations during the diurnal and vertical profiles in all lakes presented here were corrected for the bias in fluorescence increase during storage before analysis.

DOC concentrations, absorbance, metals, and statistics

DOC concentrations were measured during the field study by the platinum-catalyzed high-temperature combustion method using a Shimadzu TOC-5000 total carbon analyzer equipped with an ASI-5000 autosampler (Granéli et al. 1996). A Beckman DU 650 spectrophotometer was used for absorption measurements and the absorptivity was calculated from the relationship $2.303 \cdot abs\lambda \cdot l^{-1}$, where $abs\lambda$ is absorbance at wavelength λ and l is path length (m). Total iron and manganese concentrations were determined through inductively coupled plasma-optical emission spectrometry, using a Perkin–Elmer model 3000 DV (Tyler and Olsson 2001). The reproducibility of the analysis was ±5%. Statistics were performed in GenStat (version 6.1 for Windows). Regressions were examined between H_2O_2 production and decay and between DOC and iron and manganese concentrations.

Results and discussion

H_2O_2 production and decay under laboratory conditions

Final H_2O_2 concentrations after 8 h of artificial irradiation under laboratory conditions were significantly correlated with neither absorption coefficients at 320 nm (data not shown) nor DOC concentrations in the lakes (Fig. 1*a*). However, a tendency toward a positive correlation between DOC and H_2O_2 concentrations could be discerned among lakes with DOC concentrations below 10 mg·L^{-1}. Scully et al. (1996) studied H_2O_2 formation in a range of waters with DOC concentrations up to 20.0 mg·L^{-1}. Those authors found a positive correlation between DOC concentration and H_2O_2 formation. However, Scully et al. (1996) only used waters with DOC concentrations in the range 1.4–7.6 mg·L^{-1} in their regression between DOC concentration and H_2O_2. An aspect common to our study and the study of Scully et al. (1996) is the relatively high iron concentrations (522–1240 µg·L^{-1}; table 2 in Scully et al. 1996) in the high-DOC waters. Humic lakes usually contain high amounts of metals. Therefore, chemical decay can be very important in metal-rich waters, and the concentration of iron (Wilson et al. 2000*a*) and (or) manganese (Sunda and Huntsman 1994) may be more important than DOC concentration in explaining the variation in H_2O_2 concentration in fresh waters. Degradation of H_2O_2 through redox reactions between H_2O_2 and iron has been previously described (Voelker and Sulzberger 1996).

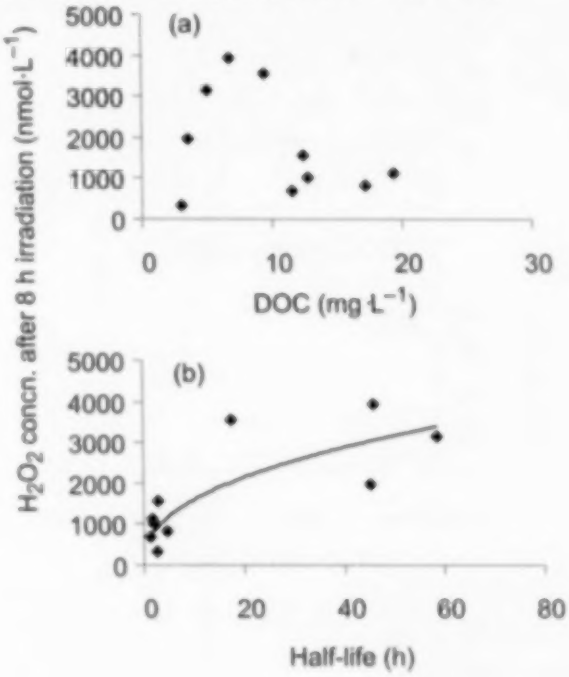

Fig. 1. Relationships between hydrogen peroxide (H_2O_2) concentration after 8 h of exposure to ultraviolet (UV) radiation in the laboratory and dissolved organic carbon (DOC) concentrations (*a*) and half-lives of H_2O_2 (*b*) ($y = 592.4x^{0.428}$, $r^2 = 0.62$).

H_2O_2 half-lives ranged between 1.4 and 58.2 h. When H_2O_2 concentrations at the end of the light incubations and H_2O_2 half-lives for the incubated waters are plotted together, a correlation between them can be seen (Fig. 1*b*). This suggests that the final H_2O_2 accumulation after 8 h of UV exposure in the studied lakes was largely determined by differing decay rates of H_2O_2. Therefore, our H_2O_2 concentration after 8 h of UV exposure may not represent real rates of H_2O_2 formation, since the final concentrations were largely offset by the low half-lives, especially those found in the metal- and DOC-rich lakes. Therefore, it is likely that the lack of relationship between DOC concentration and H_2O_2 production found in our study was due to the long incubation time

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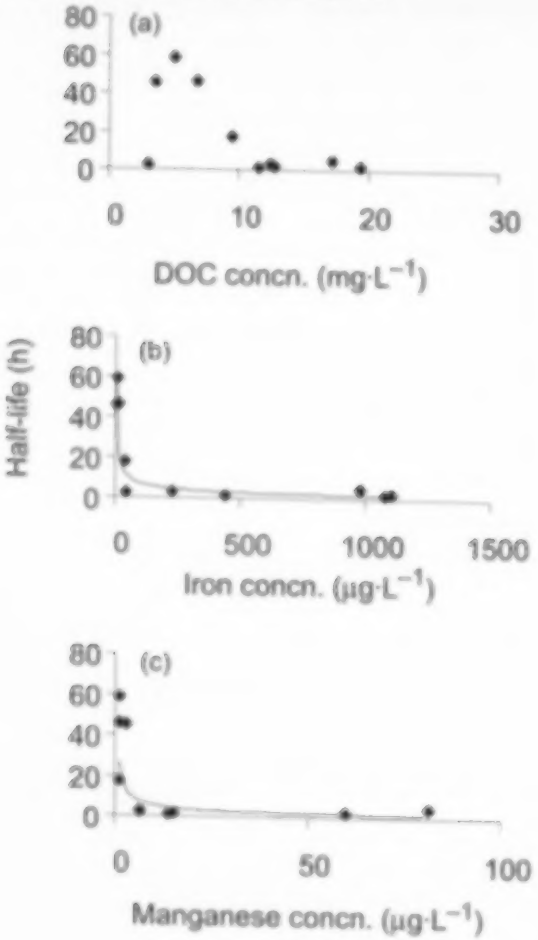
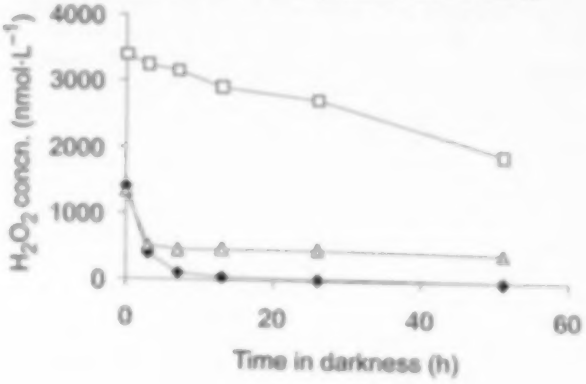
Fig. 2. Relationships between H_2O_2 decay in the laboratory and DOC (*a*), iron ($y = 98.9x^{-0.57b}$, $r^2 = 0.73$) (*b*), and manganese ($y = 28.2x^{-0.716}$, $r^2 = 0.55$) concentrations (*c*).



(i.e., measurements of H_2O_2 after 8 h of irradiation). However, even lakes with roughly similar DOC contents exhibited very different final H_2O_2 concentrations after 8 h of UV exposure (Fig. 1*a*), giving an indication that factors other than DOC may play an important role in explaining H_2O_2 production in fresh waters. We found a better negative power function relationship between H_2O_2 half-lives and metals ($r^2 = 0.73$ and 0.55 with iron and manganese concentrations, respectively) than between H_2O_2 half-lives and DOC ($r^2 = 0.16$) (Fig. 2). By studying lakes that differed in trophic status, Herrmann (1996) found that the half-life of H_2O_2 in DOC-rich waters was much shorter than in low-DOC waters, and concluded that chemical decay might be an important mechanism for explaining H_2O_2 decay in humic lakes. Two different types of H_2O_2-decay characters were detected among the lakes: (*i*) exponential (Lakes Klintsjön, Hindsen, Övingen, Homehultsjön, and Grunnen) and (*ii*) exponential followed by an asymptotic phase (Lakes Skärlen, Stråken, Stavsjön, Älgarydsjön, and Skärshultsjön)

Fig. 3. H_2O_2 concentrations in the dark (0–51 h) after 8 h of UV exposure in 3 out of 10 studied lakes. Decay of H_2O_2 in Lakes Grunnen (◆) and Hindsen (□) fitted a first-order function, while H_2O_2 concentrations in Lake Älgarydsjön (△) exhibited asymptotic decay. Values are shown as the average minus the dark control.



(Fig. 3). The asymptotic H_2O_2-decay behavior found in several of the metal-rich waters when radiation was interrupted might be explained by the complex relation between H_2O_2 and metals, since metals can form complexes, stabilize, and not react with H_2O_2 (Wilson et al. 2000*a*).

Abiotic production of H_2O_2 in the laboratory under artificial UV radiation correlated well with H_2O_2 production during the in situ incubations ($r^2 = 0.84$, $p < 0.01$), suggesting that under sterile conditions, the formation–decay equilibrium of H_2O_2 under artificial irradiation (i.e., only UV) is similar to that under natural irradiation (i.e., both PAR and UV). The in situ incubations showed, as was also indicated in the laboratory incubations, that there was no general correlation between the H_2O_2-producing capacities and the DOC concentrations of the studied lakes (data not shown).

Diurnal and vertical variation in H_2O_2 concentration under in situ conditions

The weather during the field study was predominantly warm and sunny, with integrated UV-A radiation values between 240 and 552 kJ·m^{-2} (mean ± SD = 462 ± 113 kJ·m^{-2}). Water temperatures ranged from 10 to 25 °C and the build-up of a diurnal stratification was noted on several occasions (data not shown).

The H_2O_2 concentration at the surface of the water column responded to the diurnal variation of light. The highest H_2O_2 concentrations were found in either the midday or the afternoon sampling. H_2O_2 concentrations ranged between 0 and 1041 nmol·L^{-1} (Figs. 4 and 5). Maximum concentrations were always measured at the surface (i.e., at a few centimetres depth). H_2O_2 concentrations generally decreased with depth, but high concentrations could still be observed far below the 1% depth of radiation at 380 nm, especially in the lakes with deeper epilimnia (e.g., Fig. 4*a*). This suggests that H_2O_2 produced at the surface mixes downward, and probably affects organisms and chemistry of lakes even in the layers where H_2O_2 is not produced (Scully and Vincent 1997).

The concentrations and distribution of H_2O_2 through the water column are explained by a combination of several fac-

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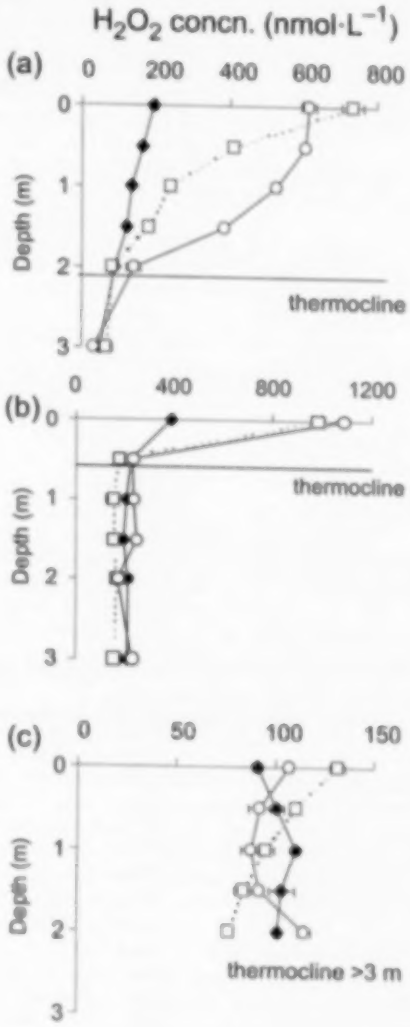
tors such as production capacity, decay rates, the depth of 1% surface irradiance in the UV range, cloud conditions, and the depth of the thermocline, among others (Cooper and Lean 1989; Kieber and Helz 1995; Herrmann 1996). H_2O_2 has previously been used as a chemical tracer for lake mixing (Scully and Vincent 1997; Scully et al. 1998). We chose some examples from our study to illustrate how several factors in combination might influence the vertical distribution of H_2O_2 in the water column in a complex way. Humic lakes such as Lake Grunnen (Fig. 4*b*) had high H_2O_2 concentrations at the surface, despite having very short H_2O_2 half-lives, as verified in the laboratory experiments (Table 2). It is likely that the high H_2O_2 concentration at the surface of Lake Grunnen is maintained by a high level of H_2O_2 formation in combination with the fact that H_2O_2 is not lost downward because of the shallow epilimnion in Lake Grunnen. Lake Stråken, on the other hand, had a much deeper epilimnion, therefore most of the H_2O_2 produced at the surface was lost to deeper layers (Fig. 4*c*). In moderate-DOC lakes (e.g., Lake Hindsen), factors such as long half-lives of H_2O_2 and moderate epilimnion depth might contribute to the high H_2O_2 concentrations detected even in layers deeper than the *z*1% for UV radiation (Fig. 4*a*).

In this study we suggest that two main factors affect the H_2O_2 concentration at the surface of fresh waters: (*i*) the depth of the epilimnion and (*ii*) the formation–decay equilibrium of H_2O_2. We used these two factors to explain the H_2O_2 concentration at the surface of the different lakes surveyed in this study. First, we corrected the H_2O_2 concentration at the surface of the different lakes at noon to an average amount of UV radiation during the period of the field sampling (i.e., the H_2O_2 concentration at an average amount of UV-A of 462 kJ·m^{-2} from 0900 to 1700). We made these corrections because the amount of irradiation received during the day varied among the lakes surveyed. Thereafter, we corrected the irradiation-normalized values for the dilution of H_2O_2 through mixing. This last correction was done simply by multiplying the irradiation-normalized surface H_2O_2 concentration by the depth of the epilimnion (Table 2). Based on this simplified model, we found a strong positive correlation between the half-lives of H_2O_2 and the surface H_2O_2 concentrations corrected by mixing depth ($r^2 = 0.81$, $p < 0.01$). We found no significant correlations between DOC concentration or absorptivity at 320 nm and surface H_2O_2 concentrations corrected by mixing depth. These results suggest that the half-lives of H_2O_2, which are strongly correlated with metals, and the depth of the epilimnion may be more important than DOC concentrations in explaining the H_2O_2 distribution in freshwater ecosystems. It should be noted that these results do not exclude the possibility that microorganisms play a role in H_2O_2 decay and distribution.

In two humic lakes, elevated H_2O_2 concentrations at 3 m depth were observed (i.e., Lakes Älgarydssjön and Skärshultsjön; Figs. 5*a*, 5*c*). The high H_2O_2 concentration at 3 m depth, comparable to surface concentrations, could hardly be explained by vertically mixed H_2O_2 produced at the surface, since temperature–depth profiles showed a clear stratification in these lakes (i.e., temperature differences of up to 7 °C between the surface and 3 m depth). Trace metal mediated production of H_2O_2 in the dark (Moffett and Zika 1987)

Fig. 4. H_2O_2 depth profile throughout the day in Lakes Hindsen (*a*), Grunnen (*b*), and Stråken (*c*). Values at 0930 (◆), 1230 (□), and 1530 (○) are shown as the mean ± standard deviation (SD) ($n = 3$). The bottom of the epilimnion is shown by the thermocline line.



is a plausible explanation of this phenomenon. Asymptotic H_2O_2-decay characters, similar to those present in the laboratory incubations, could arise also under in situ conditions in stratified waters under low light conditions (both lakes exhibited the asymptotic H_2O_2-decay character in laboratory experiments). This suggests that if production in the dark was a significant factor, then higher levels of H_2O_2 could be maintained in the lower layers of a stratified water column because of asymptotic decay of H_2O_2. In Lakes Älgarydssjön and Skärshultsjön, a cold water mass was observed at 3 m depth during the day (i.e., the temperature was several degrees lower at 1230 and 1530 than at 0930 at the same depth; Figs. 5*b*, 5*d*). It is worth noting that the decrease in temperature at 3 m depth during the day was only

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Fig. 5. H_2O_2 depth profiles (*a* and *c*) and temperature depth profiles (*b* and *d*) throughout the day in Lakes Älgarysjön and Skärshultsjön, respectively. Values at 0930 (◆), 1230 (□), and 1530 (○) are shown as the mean ± SD (n = 3).

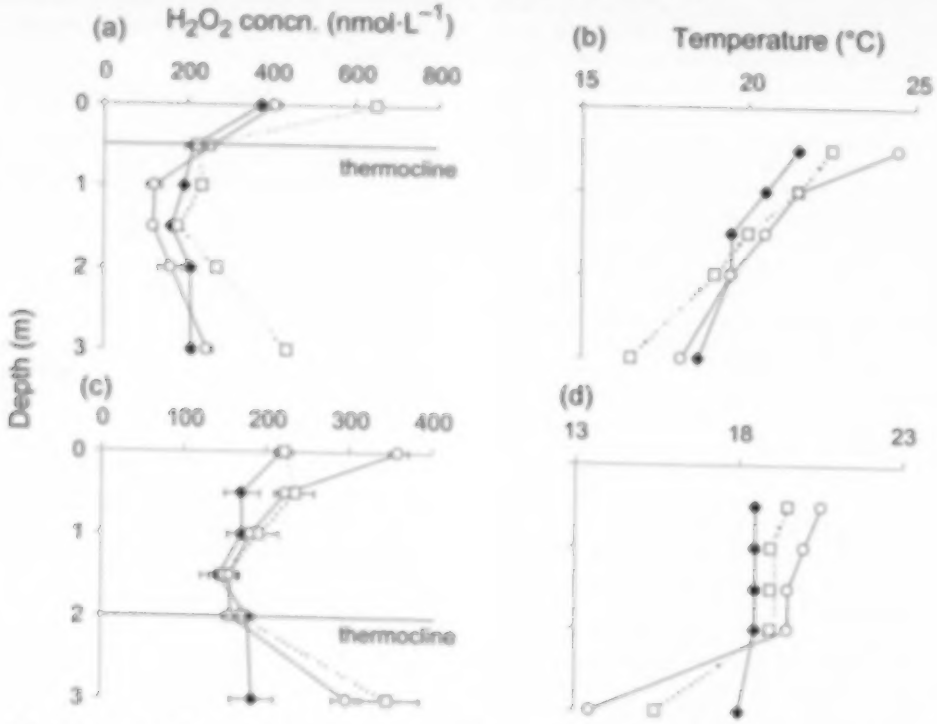

Table 2. Physical characteristics of the water column and surface H_2O_2 concentrations during field sampling, and half-lives of H_2O_2 in the studied lakes, obtained in the laboratory.

Lake	$z1\%_{380\ nm}$ (m)	Surface H_2O_2 concn. (nmol·L^{-1})[a]	Corrected H_2O_2 concn. (nmol·L^{-1})[b]	Epilimnion depth (m)	Half-life (h)	H_2O_2 × epilimnion depth[c]
Klintsjön	1.32	175	154	3.2	2.2	16.5
Skärlen	2.01	268	252	5.8	45.3	50.0
Hindsen	0.84	664	533	2.1	58.7	38.1
Övingen	0.67	239	366	3.1	45.9	38.6
Homeshultssjön	0.36	308	255	2.7	17.5	23.3
Stråken	0.19	132	126	4.0	1.4	17.2
Stavsjön	0.12	174	335	1.0	2.9	11.4
Älgarydssjön	0.14	604	505	0.5	2.1	8.6
Skärshultsjön	0.11	222	251	2.0	4.7	17.8
Grunnen	0.09	984	934	0.7	1.9	22.2

[a] H_2O_2 concentration at the surface during the sampling at 1230.
[b] H_2O_2 concentration corrected for an average UV-A of 462 kJ·m^{-2} from 0900 to 1700 (i.e., surface concentration at 1230/UV-A in that lake × 462) (see Table 1).
[c] Corrected H_2O_2 concentration (see footnote *b*) × epilimnion depth (mg H_2O_2·m^{-2}).

observed in these two lakes. The high H_2O_2 concentration, probably originating from the bottom of the lake, suggests that significant H_2O_2 production occurs under dark conditions. The same pattern has also been noted in other studies (Cooper et al. 1989*a*). Clearly, additional studies are necessary to understand the mechanisms behind H_2O_2 production in the dark, as well as its importance for H_2O_2 concentrations in deep waters of metal-rich lakes.

Based on the results of this study, we conclude that H_2O_2 distribution in boreal lakes can be highly variable, with no general correlation with DOC concentrations. Previous observations by Scully et al. (1995) have indicated a lack of correlation between DOC and H_2O_2 concentrations on an areal basis in Canadian lakes. We have shown in this study that measured H_2O_2 concentrations were largely determined by the differing decay rates of H_2O_2 and the mixing depth of the water column. In addition, we have shown that metals might substantially affect the decay of H_2O_2, and should be considered in further studies on the distribution of H_2O_2 in fresh waters, especially humic lakes.

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Movement patterns in inland cutthroat trout (*Oncorhynchus clarki utah*): management and conservation implications

Amy J. Schrank and Frank J. Rahel

Abstract: Knowledge of movement patterns is critical to the management and conservation of inland salmonids. We studied the movements of Bonneville cutthroat trout (*Oncorhynchus clarki utah*) in a drainage in western Wyoming, USA. Our objectives were to (*i*) characterize the postspawning movement patterns of adult Bonneville cutthroat trout, (*ii*) contrast postspawning and summer movement patterns, and (*iii*) identify factors that disrupt the movements of Bonneville cutthroat trout. Our data showed that postspawning movements of Bonneville cutthroat trout formed a continuum, with fish moving from 0.5 to 82.0 km. Postspawning distance was positively related to fish length. Despite the wide range of movement observed during the spring, fish did not move more than 0.5 km during the summer. A road culvert and an irrigation diversion dam did not seem to pose barriers to the upstream movement of Bonneville cutthroat trout to headwater spawning areas in the spring. However, 23% of radio-tagged fish in 2000 moved into the irrigation diversion ditch as they moved downstream after spawning and subsequently died there. Maintaining drainage connectivity is an important conservation concern for trout populations such as this one, where fish move between complementary spawning and summer habitats.

Résumé : Une connaissance des patterns de déplacement des salmonidés à l'intérieur du continent est essentielle à leur conservation et leur gestion. Nous avons étudié les déplacements de la truite fardée de Bonneville (*Oncorhynchus clarki utah*) dans un bassin versant de l'ouest du Wyoming, États-Unis. Nos objectifs étaient (*i*) de décrire les patterns de déplacement après la fraye des truites fardées de Bonneville adultes, (*ii*) de comparer les patterns de déplacement après la fraye et ceux de l'été et (*iii*) d'identifier les facteurs qui perturbent les déplacements de la truite fardée de Bonneville. Nos données indiquent que les déplacements des truites fardées de Bonneville après la fraye forment un continuum, les poissons se déplaçant de 0,5 à 82,0 km. La distance parcourue après la fraye est fonction de la longueur du poisson. Malgré l'étendue importante des déplacements enregistrés au printemps, les poissons ne se déplacent pas plus de 0,5 km en été. Un ponceau de route et un canal de dérivation d'irrigation ne semblent pas former de barrière à la remontée des truites fardées de Bonneville vers les sites de fraye d'amont au printemps. Cependant, 23 % des poissons porteurs d'émetteurs radio en 2000 ont pénétré dans le fossé de dérivation d'irrigation lors de leur descente vers l'aval après la fraye et y sont morts éventuellement. Le maintien de la connectivité du réseau hydrographique est un problème important pour la conservation d'une population de truites comme celle-ci, chez laquelle les poissons se déplacent entre des habitats de fraye et des habitats d'été qui sont complémentaires.

[Traduit par la Rédaction]

Introduction

Movement is an integral part of the life history of many stream fishes. If most individuals in a population are sedentary (Gerking 1959; Hughes 2000), then a relatively small length of stream may provide sufficient habitat to meet all life-history needs. Preserving movement corridors and maintaining watershed connectivity may not be as critical for such species as it is for other species that undergo large-scale movements and utilize different habitats located in different parts of the watershed (Young 1994; Brown and Mackay 1995; Swanberg 1997). For such wide-ranging species, human-caused fragmentation of rivers can reduce population viability (Rieman and Dunham 2000). Fragmentation in streams causes declines in fish populations by interrupting movements to and from critical sites that fish must reach to complete their life history (Schlosser 1995). Consideration of the time scales over which movement occurs is also necessary. From the perspective of habitat selection and use, knowledge of movement within the lifetime of an individual is important, whereas from a metapopulation-dynamics perspective, understanding movement patterns

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over generations or even longer time scales is critical. Where stream-fish species fall along this continuum of movement has generated a lively debate among fisheries biologists (Gowan et al. 1994; Rodriguez 2002) because of the importance of movement patterns to management and conservation of stream fishes (Fausch et al. 2002; Webster et al. 2002).

The recent adoption of a landscape or "riverscape" perspective in stream ecology emphasizes the need to understand fish movement patterns in relation to the spatial arrangement of habitats in a drainage (Fausch et al. 2002). The spatial arrangement of habitats is important because the need for fish to move, and consequently the impacts of barriers to movement, depend on the degree of habitat complementation within stream reaches. Habitat complementation refers to the spatial proximity of different but non-substitutable habitats required by a species to complete its life cycle (Dunning et al. 1992; Schlosser 1995). When habitat complementation is low, critical habitats are located relatively long distances apart. Consequently, an individual must expend more energy to reach required habitat, perhaps exposing itself to increased risk of predation or other sources of mortality along the way (Dunning et al. 1992; Schlosser 1995). Furthermore, interruption of movement to and from complementary habitats will prevent individuals from completing their life cycle and ultimately cause declines in populations. Studying movement patterns can identify which portions of a stream are most critical for maintenance of a population (Rieman and Dunham 2000). The preservation of connectivity among habitats is especially critical to populations that face fragmentation from road crossings, reservoir development, water withdrawal, or introduction of non-native species.

In addition to knowing the extent of movement in a population, it is important to know how population demography affects movement patterns. There is evidence that larger fish move longer distances (Clapp et al. 1990; Young 1994). Long-distance movers may be larger as a result of greater growth potential in higher order reaches where they can become piscivorous (Behnke 1992; Bunnell et al. 1998; Colyer 2002). Or fish may be moving to find increased space, better physical habitat, or more tolerable thermal regimes (Kahler et al. 2001; Roni and Quinn 2001; Schrank et al. 2002). Because fecundity increases exponentially with body size, large fish that may spend most of their lives in main-stem areas potentially contribute more genetic material to the next generation than small fish that live in smaller tributaries. Examining reasons for variation in movement patterns related to fish size may help indicate how habitat requirements for individuals within a population vary and how conservation efforts can best target all portions of the population.

The objectives of our study were to (*i*) characterize the postspawning movement patterns of adult Bonneville cutthroat trout (*Oncorhynchus clarki utah*), (*ii*) contrast postspawning and summer movement patterns, and (*iii*) identify factors that disrupt the movements of Bonneville cutthroat trout. Fausch et al. (2002) indicated the need for collecting spatially continuous data on stream fishes. By using radiotelemetry we were able to gain a continuous view of Bonneville cutthroat trout postspawning and summer movements throughout an entire watershed and position this population along the sedentary–migratory continuum. Angermeier et al. (2002) indicated that knowledge of spatiotemporal dynamics of fish movement is lacking. We examined movement patterns across spring and summer to describe some of the temporal variation that exists in movement patterns of individual fish. Finally, we sought to identify potential barriers to movement and the consequences of these barriers for the fish population. Fausch et al. (2002) indicated that rare features in a drainage such as a barrier can be disproportionately important to stream-fish populations. By tracking fish continuously through spring and summer we were able to determine if barriers prevented movement among complementary habitats in this watershed.

Methods

Study site

This study took place in the Thomas Fork drainage (584.2 km^2) of the Bear River in Lincoln County, Wyoming, and Bear Lake County, Idaho, USA (Fig. 1). The climate in this drainage consists of cold snowy winters and hot dry summers. Huff, Little Muddy, and Coal creeks flow through land heavily impacted by livestock grazing. Consequently these creeks have little riparian vegetation to shade the stream. In recent years the Wyoming Game and Fish Department and the US Bureau of Land Management have been working to restore habitat conditions for Bonneville cutthroat trout in these tributaries (Binns and Remmick 1994). Water Canyon Creek flows through land that is not as heavily impacted by grazing, and it has a dense willow riparian area and numerous beaver dams along its length. The riparian area of the Thomas Fork main stem in Idaho is dominated by hay agriculture. During the summer, much of the Thomas Fork is diverted for irrigation, primarily through the Taylor Ditch (Fig. 1).

The Thomas Fork drainage contains native populations of Bonneville cutthroat trout and no non-native salmonids. The Bonneville cutthroat trout, along with other native subspecies of cutthroat trout throughout the western USA, has experienced severe declines as a result of hybridization with non-natives and habitat degradation and fragmentation, and is considered a species of concern by state and federal management agencies (Young 1995; US Fish and Wildlife Service 2001).

Objective 1: to characterize the postspawning movement patterns of adult Bonneville cutthroat trout

We used radiotelemetry to determine the distribution of displacement distances as fish moved from spawning locations to summer locations. A total of 62 fish were implanted with radio transmitters during spawning (16 May – 8 June) in 1999, 2000, and 2001 in Coal, Huff, Little Muddy, and Water Canyon creeks (Table 1, Fig. 1). Fish were captured by electrofishing and anesthetized with clove oil (Anderson et al. 1997). Depending on fish weight, a transmitter with an external antenna weighing 2.9 or 3.6 g (Advanced Telemetry Systems Inc., Isanti, Minnesota, USA) or 8.9 g (Lotek Wireless Inc., Newmarket, Ontario, Canada) was surgically implanted into the ventral body cavity of each fish, just anterior to the pelvic girdle (Adams et al. 1998). In all fish the radio transmitter weight in air did not exceed 2% of the body weight of the fish (Adams et al. 1998). Fish were ground-

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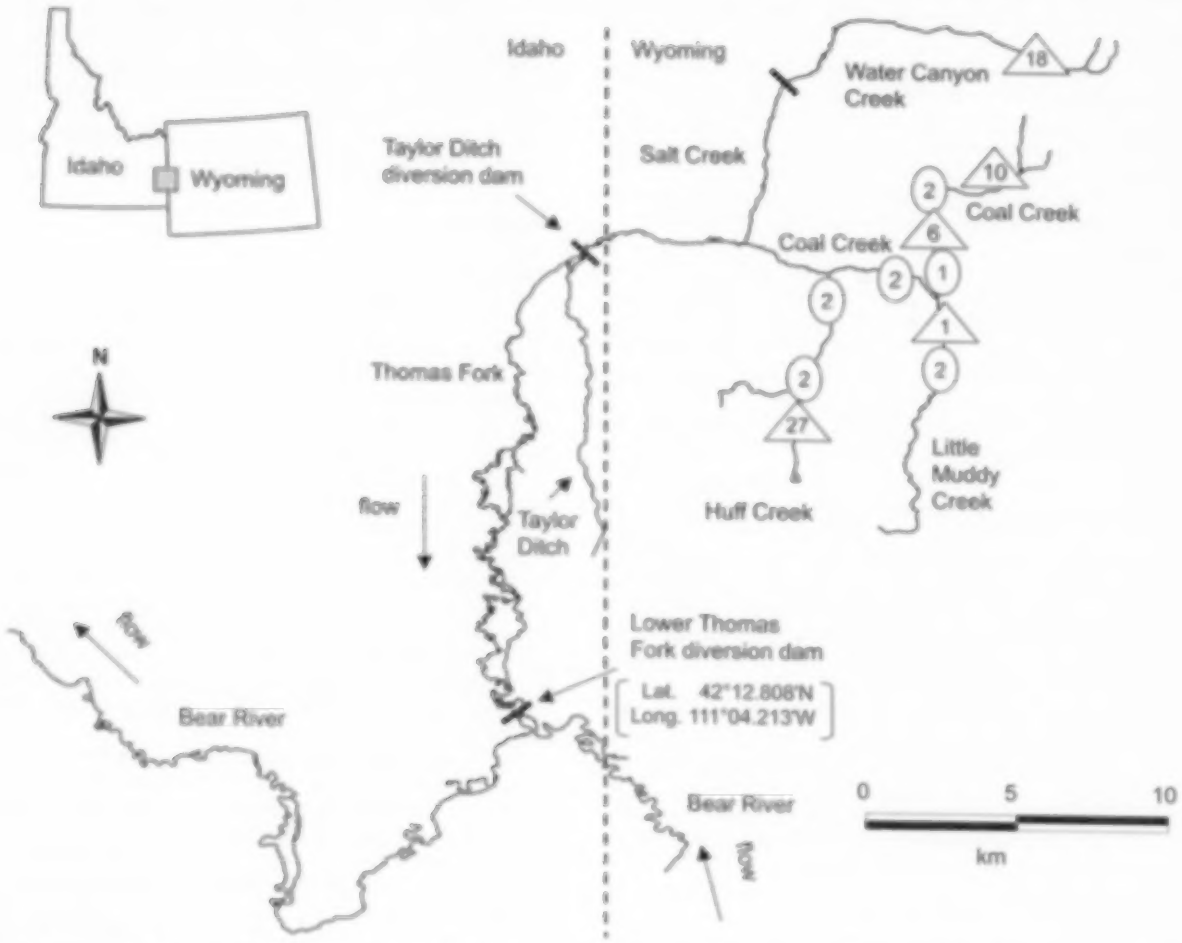
Fig. 1. Map of the Thomas Fork drainage of the Bear River in Lincoln County, Wyoming, and Bear Lake County, Idaho, USA. Triangles indicate locations where 62 fish were radio-tagged during spawning in 1999, 2000, and 2001. Numbers in the triangles represent the number of fish tagged at that location. Ovals show locations where 11 fish were radio-tagged during the summer of 1999 to examine summer movement patterns (objective II). Numbers in the ovals represent the number of fish tagged at each location.



tracked with an Advanced Telemetry Systems R2000 receiver operating at frequencies of 150.000–151.999 MHz and a four-element Yagi antenna. During spring 2000 and 2001 fish were tracked both from the ground and using at least monthly aerial flights, but were ground-tracked only in 1999. When a fish was located its position was recorded using a Global Positioning System (GPS).

Adult fish captured on the spawning grounds in the spring were assumed to have spawned. Twelve of the 62 implanted fish died in the spawning tributaries before the end of June and were eliminated from the study. These fish were eliminated because it was impossible to determine how far they would have moved after spawning. The 50 fish that remained were tracked until death or late summer, whichever came first. In 1999 two fish were lost as they moved downstream after spawning. Because we were not using flights to relocate fish during 1999 and the Thomas Fork main stem was not easily accessible by foot, we assumed that these fish continued downstream beyond the area we could track on the ground. However, they could have been removed by predators, therefore we used the last known location of these fish to estimate their movement distance.

Movement distances of each radio-tagged fish were calculated from GPS locations using a geographic information system with ArcView® 3.2 and ArcInfo® 8.1 software (Environmental Systems Research Institute, Inc., Redlands, California, USA). Total postspawning displacement distance was recorded from the most upstream location of a fish (where it was assumed to have spawned) to the location to which it had moved as of 30 days after the spawning season ended each year. We chose 30 days because all fish that left their spawning tributary had done so by then. All postspawning movement distances reported refer to total displacement distance.

In addition to examining the distribution of displacement distances, we examined the relationship between postspawning movement patterns and fish total length. We used simple linear regression to examine the relationship between post-

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Table 1. Summary of total lengths and weights of fish implanted with radio transmitters during 1999, 2000, and 2001.

	N	Mean total fish length (mm)[a]	Mean fish weight (g)[a]	Implantation dates
In tributaries of the Thomas Fork				
Spring 1999	7	369 (290–445)	481 (214–759)	26 May – 8 June
Spring 2000	40	389 (352–503)	535 (422–1269)	16 May – 5 June
Spring 2001	15	305 (236–345)	264 (180–377)	18 May – 25 May
All springs	62	367 (236–503)	464 (180–1269)	—
Summer 1999	11	314 (270–384)	305 (187–491)	24 June – 10 July
In the Thomas Fork main stem				
2000	10	399 (369–493)	575 (435–1113)	8 May, 15 May, 19 September, 25 October

Note: Spring implantation was carried out during the spawning season and summer implantation after the spawning season ended.
[a]Values in parentheses are ranges.

spawning movement distance (in kilometres) and fish total length (in millimetres). To eliminate fish that may have died before reaching summer locations, we only used fish that were alive on 1 July in this analysis ($N = 17$).

Objective II: to contrast postspawning and summer movement patterns

To address objective II we examined mobility patterns across seasons using two approaches. First, we compared histograms of spring versus summer displacement distances for 12 of the 50 fish originally tagged in the spring that we were able to monitor through the subsequent summer. These 12 fish were tracked between 3 and 21 times during the summer. Second, in addition to the 50 fish radio-tagged in the tributaries in the spring, 11 other fish were radio-tagged in Coal, Huff, and Little Muddy creeks during the summer of 1999 using the method described above (Table 1, Fig. 1). These 11 fish were tracked every other day from at least 1 July through 31 August 1999. This intensive tracking allowed us to determine summer movement patterns at a finer temporal scale than was possible for the fish radio-tagged during the spring. Summer displacement distance was calculated from the most upstream to the most downstream location of each fish during the period 1 July to 31 August 1999. All summer movement distances reported in the study refer to total displacement distance.

Objective III: to identify factors that interrupt Bonneville cutthroat trout movement

In the course of monitoring movements of radio-tagged fish we paid special attention to the Salt Creek highway culvert and the Taylor Ditch diversion dam to determine if they were barriers to fish movement. The Salt Creek highway culvert was a round corrugated-metal culvert 16 m in length, 1.5 m in diameter, and with a drop of 0.15 m from culvert lip to water. At the end of the culvert was a 1.5 m deep pool, and maximum water velocities in the culvert were at least 1.5 $m \cdot s^{-1}$ during spring runoff. The Taylor Ditch diversion dam had a maximum height of 1.1 m during spring flows and there were no pools from which fish could stage before attempting to pass this structure. We implanted fish with radio transmitters below these barriers in 2000; eight fish were implanted downstream of both the diversion dam and the highway culvert, and two fish were implanted upstream of the diversion dam but downstream of the highway culvert (Table 1, Fig. 1). Fish movements were monitored to determine if fish moved upstream past these two potential barriers.

We also used visual implant (VI) tags (Haw et al. 1990) to determine whether fish were able to pass potential barriers. Between 4 August 1998 and 2 July 2001, 1235 fish were implanted with VI tags below the large highway culvert on Salt Creek. These included 403 fish that were implanted with VI tags below the Taylor Ditch diversion dam (Fig. 1). Reaches upstream of these barriers were sampled from May 1999 through September 2001 to determine if any fish tagged below these structures were able to pass them successfully.

Results

Objective I: to characterize the postspawning movement patterns of adult Bonneville cutthroat trout

Movement distances ranged from less than 0.5 km to 82.0 km downstream from spawning locations (Fig. 2). No fish moved upstream. Postspawning movement distances formed a continuum, with two fish even leaving the Thomas Fork and entering the Bear River system (Fig. 3). There was a significant positive linear relationship between postspawning distance moved and fish length ($N = 17$, $r^2 = 0.38$, $P = 0.009$, $df = 16$, $\alpha = 0.05$, Fig. 4).

Objective II: to contrast postspawning and summer movement patterns

Movement patterns of 12 fish radio-tagged during spawning in spring of 1999, 2000, or 2001 were monitored throughout the subsequent summer. Despite the range of movement observed after spawning (up to 82.0 km), the same fish showed little movement during the summer at a scale larger than 0.5 km (Figs. 5*a* and 5*b*). Because some of these fish were located only a few times, we also examined summer movement data for the group of 11 fish radio-tagged between 24 June and 10 July 1999 and located every other day until at least 10 September 1999. None of these 11 fish had a displacement distance of more than 0.3 km throughout the summer (Fig. 5*c*).

Objective III: to identify factors that interrupt fish movement

One VI-tagged fish and one radio-tagged fish moved above both the Salt Creek highway culvert and the Taylor Ditch diversion dam (Table 2, Fig. 6). An additional VI-tagged fish was observed to have moved successfully upstream through

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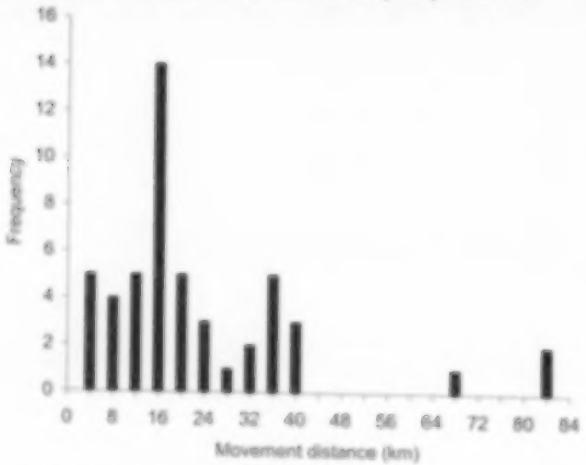
Fig. 2. Postspawning movement distances varied from 0.5 to 82.0 km ($N = 50$). The large peak at 16 km represents 21 fish that moved to lower Salt Creek and subsequently died there.



the Salt Creek highway culvert. Finally, seven VI-tagged fish and two radio-tagged fish moved upstream past the Taylor Ditch diversion dam. The maximum water velocity through the Salt Creek highway culvert was at least 1.5 $m \cdot s^{-1}$ during the spring.

In addition to monitoring barriers to upstream movements, we also monitored disruption of downstream movement. No radio-tagged fish entered the Taylor Ditch in 1999 ($N = 7$) or 2001 ($N = 15$). However, in 2000, 9 of 40 (23%) fish that were radio-tagged on the spawning grounds eventually moved downstream into the Taylor Ditch and subsequently died there when irrigation flows ceased in late summer (Fig. 3).

Discussion

Understanding the movement patterns of inland salmonids is critical to preserving and managing populations. However, there has been much debate about where inland salmonids fall on the migratory–resident continuum (Gowan et al. 1994). A classic example of migration involves cutthroat trout that live in Yellowstone Lake most of the year, migrate up into tributaries in the spring to spawn, and return to the lake immediately after spawning (Varley and Gresswell 1988). At the other extreme are populations of salmonids in streams where fish are considered to be highly sedentary throughout their lives (Miller 1954; Young 1998). However, even salmonids living in small streams may move farther upstream to find spawning sites on relatively small scales, indicating that many salmonids are migratory at some level (Soloman and Templeton 1976; Young 1994, 1996). Our data showed that Bonneville cutthroat trout that moved extensively after spawning moved over a much smaller range during the summer. Other researchers have also noted this pattern (Swanberg 1997; Hilderbrand and Kershner 2000; Schmetterling 2001), and therefore characterizing movements of salmonids during one season will not necessarily allow movement patterns during other seasons to be predicted.

The extent of migratory behavior within a population appears to depend on the degree of habitat complementation that exists in a drainage (Dunning et al. 1992; Schlosser 1995). If all the habitats fish need to complete their life history are in close proximity, then movement will be minimal. However, if spawning, feeding, and overwintering habitats are located far apart, then movement distances will be high (Schlosser 1995). In the Thomas Fork drainage, we never observed spawning activity in the main stem; however, spawners were frequently observed in the tributaries. Furthermore, White (2003) found many young-of-the-year Bonneville cutthroat trout in the tributaries but few in the main stem of the Thomas Fork. Our data showed that of 50 fish radio-tagged on the spawning grounds, 75% moved out of the tributaries within 30 days of spawning. Clearly, fish in the Thomas Fork need the combination of main-stem habitat for feeding and overwintering and tributary habitat for spawning. Furthermore, for some fish these habitats are located a long distance apart, requiring a high degree of movement. Rather than focusing on the proportion of mobile or sedentary fish in a population (Heggenes et al. 1991; Hughes 2000; Rodriguez 2002), determining the range of movement and why movement occurs will offer more insight into which habitats are critical for population persistence.

Often, researchers model fish movement by assuming that fish move randomly through the environment following a model of passive diffusion (Rodriguez 2002). Data from our study indicate that cutthroat trout postspawning movements do not follow a negative exponential function suggestive of passive diffusion. Hilderbrand and Kershner (2000) also noted that movement of Bonneville cutthroat trout in their study stream did not fit a model of passive diffusion. This suggests that cutthroat trout in these streams are exhibiting ranging behavior (Dingle 1996) in which they move downstream after spawning and stop when they reach suitable summer habitats. In our case, the movement data have a peak at 16 km representing a large number of fish that moved downstream to lower Salt Creek. These fish resided in a reach with an exceptionally deep pool and extensive overhanging vegetation that was rare in upstream reaches or in tributary streams. Interestingly, despite the apparent high quality of the habitat, most of the fish in this reach died during the remainder of the summer. We suspect that this mortality was caused by river otters (*Lutra canadensis*) because we saw otter scat and tracks in the area and located some of the radio transmitters in heavy brush far away from the stream. Thus, although we usually consider that movement to downstream deep-water habitat reduces the exposure of trout to predators, there may be localized situations where predation remains a significant source of mortality.

One of the patterns apparent in this study was that larger fish tended to move farther after spawning than smaller fish. Several researchers have found that movement distances increase with fish length for brown trout (*Salmo trutta*) (Clapp et al. 1990; Young 1994; Bunnell et al. 1998). In contrast, Hilderbrand and Kershner (2000) found no relationship between distance moved and fish length in their study of Bonneville cutthroat trout in a headwater stream in Idaho. This discrepancy with our results is probably due to the absence of large fish in the Idaho study, where the maximum length of fish captured (300 mm total length) was less than in our study (503 mm total length). It has been suggested that fish move downstream after spawning because of greater

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Fig. 3. Postspawning locations of 50 fish that were initially radio-tagged on spawning grounds in the headwaters of Huff, Coal, Water Canyon, and Little Muddy creeks during 1999, 2000, or 2001. The number in each oval indicates the number of fish found at that location.

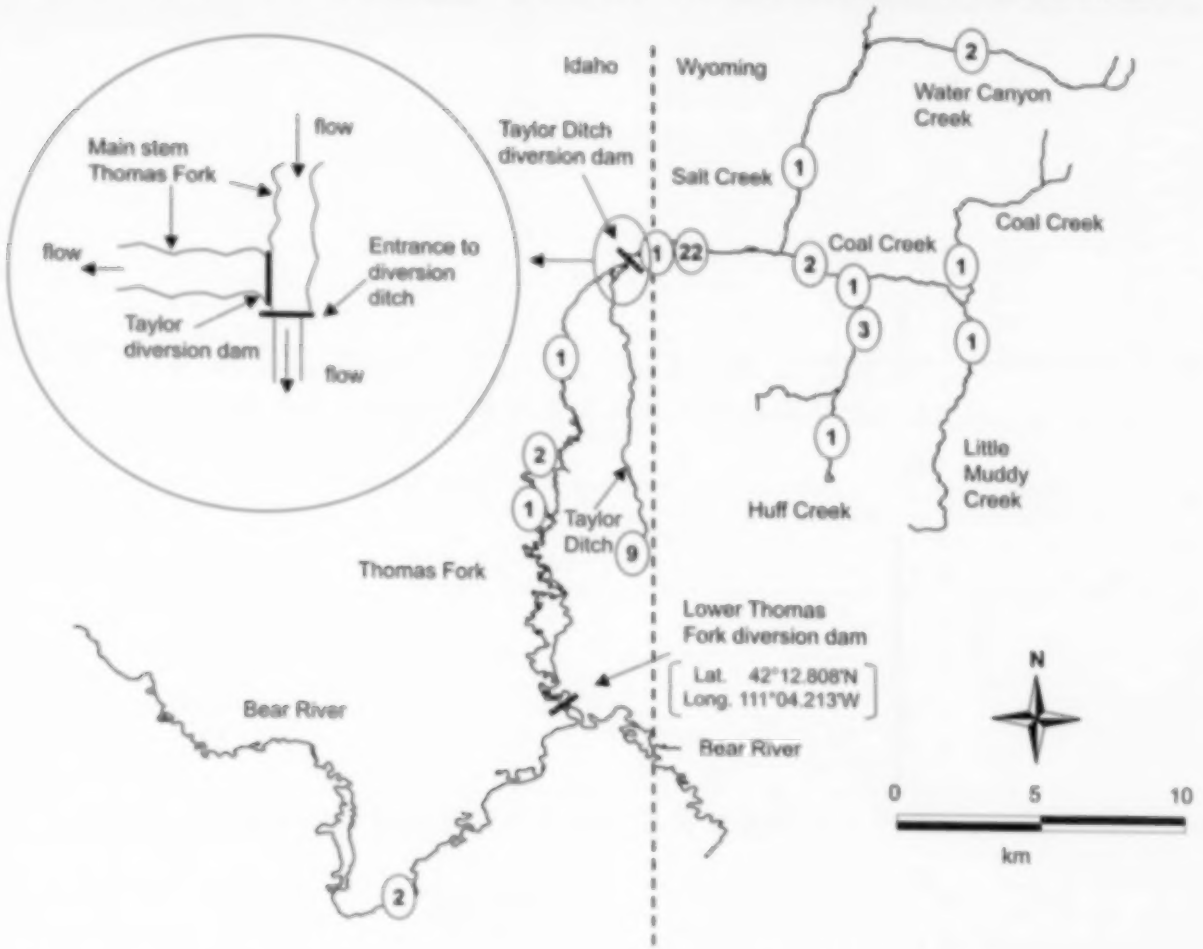
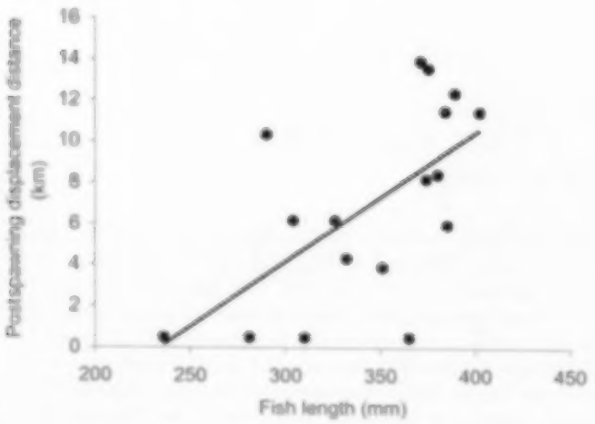


Fig. 4. Significant positive relationship between movement distance and fish total length, based on fish assumed to have reached summer locations ($y = 0.06x - 14.71$, $r^2 = 0.38$, $P = 0.009$, $N = 17$.



growth potential in higher order stream reaches, including the opportunity to become piscivorous (Clapp et al. 1990; Behnke 1992; Bunnell et al. 1998). In the Thomas Fork, piscivory by large trout would require movement to the farthest downstream reaches, where small prey fishes, especially cyprinids, become abundant (Colyer 2002).

If fish are not moving downstream to find food it is possible that they are simply searching for increased habitat space (Kahler et al. 2001; Roni and Quinn 2001). Headwater tributaries of the Thomas Fork tend to be shallow, with few deep pools (Binns and Remmick 1994). Large fish that return from spawning later may have to continue downstream until they encounter suitable habitat space lower in the drainage. Gowan and Fausch (1996) showed that salmonids will move relatively long distances (>500 m) until they encounter suitable habitat and then will tend to remain in these areas. If fish are moving to find better habitat, this suggests that habitat restoration would increase fish abundance in the tributaries by increasing habitat complementation. For example, Binns and Remmick (1994) examined Bonneville cutthroat trout populations before and after habitat improvement on

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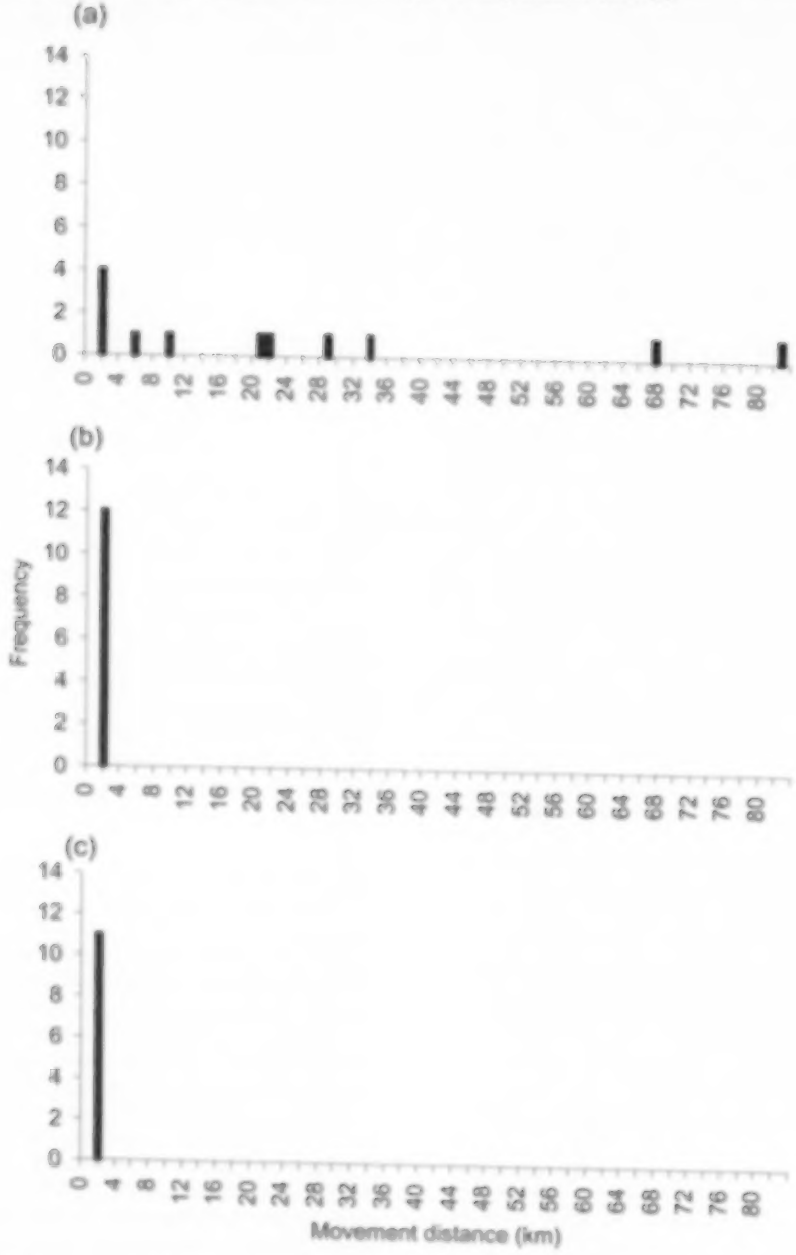
Fig. 5. Frequency histograms of movement distances for postspawning movements of 12 fish radio-tagged during spawning (16 May through 8 June 1999–2001) (*a*); summer movements (1 July through 31 August 1999–2001) of the same 12 fish (*b*); and summer movements (1 July – 31 August 1999) of 11 additional fish radio-tagged during summer 1999 (*c*).



Huff Creek. Large cutthroat trout (>15 cm total length) increased from 22·km^{-1} before habitat improvement to 106·km^{-1} 11 years after habitat improvement, suggesting that habitat limited the abundance of large fish in the tributaries. Habitat restoration has been historically concentrated in the tributaries in the Thomas Fork drainage, but could include improvement of spawning substrates in lower portions of the drainage. Habitat improvement is likely an effective strategy for increasing habitat complementation and thus increasing the carrying capacity for large trout in this drainage.

In addition to understanding the temporal variation in movement patterns, determining if there are barriers to movement is critical to maintaining inland salmonid populations. Although we thought that the Salt Creek highway culvert and the Taylor Ditch diversion dam had the potential to be major barriers to upstream movement in the Thomas Fork,

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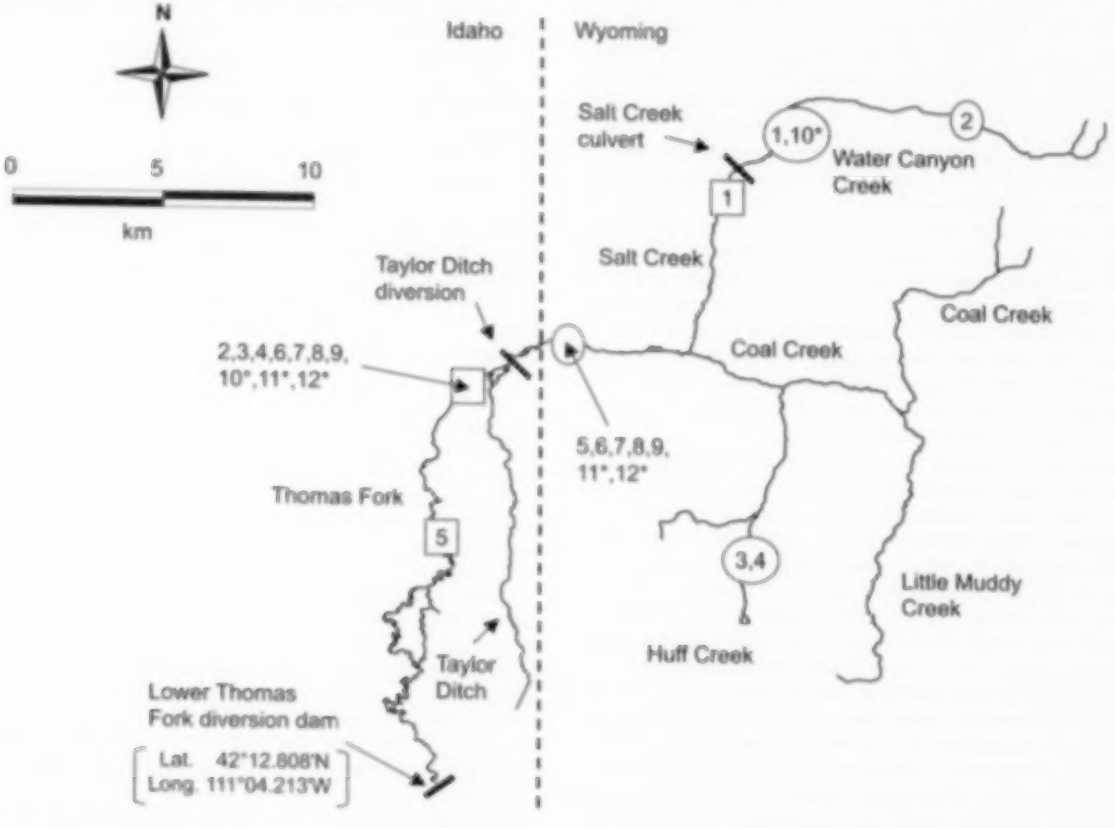
Table 2. Summary of fish recorded moving past the Salt Creek highway culvert and (or) the Taylor Ditch diversion dam.

ID No. and tag type[a]	Date implanted	Total length (mm)	Weight (g)	Date recaptured	Total length (mm)[b]	Weight (g)[b]	Structure passed[c]
1, VI	9 June 1999	372	508	3 Aug. 1999	368	451	Culvert
2, VI	6 Oct. 1999	400	646	27 May 2000	402	529	Both
3, VI	6 Oct. 1999	352	412	18 May 2000	356	404	Dam
4, VI	6 Oct. 1999	360	510	18 May 2000	361	454	Dam
5, VI	6 Oct. 1999	212	93	2 July 2001	263	154	Dam
6, VI	27 Apr. 2000	160	32	14 Aug. 2000	200	73	Dam
7, VI	27 Apr. 2000	246	120	14 Aug. 2000	266	160	Dam
8, VI	27 Apr. 2000	204	70	14 Aug. 2000	232	108	Dam
9, VI	8 May 2000	240	114	14 Aug. 2000	264	140	Dam
10, radio	8 May 2000	369	435	24 May 2000	×	×	Both
11, radio	8 May 2000	418	614	9 May 2000	×	×	Dam
12, radio	25 Oct. 2000	400	537	26 May 2001	×	×	Dam

[a]VI, visual implant tag; radio, radio transmitter.
[b]A × denotes missing data.
[c]"Culvert" indicates that a fish moved upstream past the Salt Creek highway culvert, "dam" indicates that a fish moved upstream past the Taylor Ditch diversion dam, and "both" indicates that a fish moved upstream past both structures.

Fig. 6. Map showing locations of fish implanted with visual implant (VI) and radio tags below the Salt Creek highway culvert and (or) the Taylor Ditch diversion dam and the locations to which these fish moved upstream of these structures. Squares indicate locations below potential barriers at which fish were radio- and VI-tagged and subsequently relocated upstream of these structures (N = 12). An asterisk denotes a radio-tagged fish. Numbers inside or pointing to squares indicate the identification number(s) of the fish tagged there. Ovals indicate recapture locations of fish originally tagged downstream of barriers. Numbers inside or pointing to circles indicate the identification number(s) of the fish recaptured there.



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some fish were able to navigate these structures. Belford and Gould (1989) modeled the ability of rainbow trout (*Oncorhynchus mykiss*) to swim through highway culverts and predicted that the maximum current speed passable by trout (161–393 mm total length) would be 1.32 $m \cdot s^{-1}$ for a 10 m long culvert. However, fish that passed through the Salt Creek highway culvert swam against velocities of at least 1.5 $m \cdot s^{-1}$ over a distance of 16 m. This discrepancy likely reflects the fact that fish in our study were generally longer (369–400 total length) than those used to develop the models of Belford and Gould (1989). The fish that moved above the Thomas Fork irrigation diversion dam had to leap a maximum of 1.1 m during spring runoff, which is within the leaping ability of salmonids (Bjornn and Reiser 1991). Although some fish made it past each of the potential migration barriers in the Thomas Fork, we do not know what proportion of the population may have been unable to get past them.

Surprisingly, disruption of downstream movement was more of an issue than disruption of upstream movement. Upstream migration of Bonneville cutthroat trout coincides with high spring flows that facilitate jumping over or circumventing potential barriers (Bjornn and Reiser 1991). Downstream migration occurs during lower flows, when water withdrawal increases the likelihood of fish following major currents and being diverted into dead-end canals. When the timing of irrigation along the lower Thomas Fork coincides with the time fish are returning from spawning, as it did during the spring of 2000, fish are vulnerable to being trapped in the Taylor Ditch diversion. There is no screen or other device on this ditch to prevent fish access, and fish moving downstream may be directed into the ditch rather than down the actual river channel. Of the 40 fish implanted with radio transmitters during the spring of 2000, 23% were trapped in the Taylor Ditch and subsequently died there. Given that estimates of mortality after spawning range from a minimum of 38% for westslope cutthroat trout (*Oncorhyncus clarki lewisi*) (Schmetterling 2001) to 89% for Lahontan cutthroat trout, *Oncorhynchus clarki henshawi* (Vinyard and Winzeler 2000), an additional 23% mortality could have severe consequences for cutthroat trout populations. This supports the contention of Fausch et al. (2002) that a rare feature in the environment such as a barrier can have a disproportionate effect on a stream fish population.

Extensive movements such as those we observed in cutthroat trout have important implications for both management and conservation of fish. From a management perspective, vulnerability to harvest may vary among habitats. For example, large trout can be highly vulnerable to angling during the period they spend in shallow tributary streams and thus, seasonal closures, increased size limits, or reduced creel limits may be needed to reduce harvest. Management activities that increase habitat complementation, such as restoration of pool habitat in shallow tributary streams or creation of spawning areas lower in the drainage, can increase local population size by reducing the need for fish to emigrate to upstream or downstream reaches. From a conservation perspective, maintaining connectivity between complementary habitats such as spawning, summer, and overwintering areas will ensure that fish have access to all habitats necessary to sustain the population. Furthermore, it is important to note that movement pathways can be disrupted not only by blocking upstream spawning movements but also by connecting to sink habitats, such as irrigation canals, as fish return downstream.

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Temporal changes in nitrogen and phosphorus codeficiency of plankton in lakes of coastal and interior British Columbia

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Abstract: Plankton nutrient limitation and deficiency were assessed in six coastal and four interior lakes and reservoirs in British Columbia. Ultimate nutrient limitation was defined as occurring over longer time scales (months to years) and represented the potential attainable biomass or yield. Proximate nutrient deficiency reflected plankton physiological status and, therefore, represented potential limitations of instantaneous growth rates. All lakes and reservoirs were considered to be ultimately P-limited according to total N to total P ratios (TN:TP). However, both P and N deficiencies were found to occur at the same time, suggesting that when deficiency occurs, codeficiency is common. The <3 μm size fraction accounted for a large proportion of P debt, whereas the >3 μm size fraction accounted for most of the ammonium-enhanced response. Thus, plankton size is important for understanding nutrient deficiencies in plankton communities. Our results stress (i) the importance of measuring proximate deficiencies at greater temporal resolution, (ii) that N and P were commonly found to be codeficient, (iii) the need to define nutrient limitation and deficiency in the context of the method used, and (iv) that several concurrent measures of deficiency are required to assess the nutrient status of plankton communities.

Résumé : Nous avons évalué les carences et les restrictions nutritives du plancton dans des lacs et des réservoirs de Colombie-Britannique, six dans la région côtière et quatre à l'intérieur des terres. Nous avons défini la restriction nutritive extrême comme celle qui se produit sur une échelle de temps plus longue (mois à années) et qui représente la biomasse ou le rendement potentiel réalisable. La carence nutritive proximale reflète le statut physiologique du plancton et, ainsi, elle représente les restrictions potentielles des taux instantanés de croissance. Nous avons considéré tous les lacs et réservoirs comme limités en fin de compte par P en fonction des rapports de N total sur le phosphore total (TN:TP). Cependant, des carences de P et de N peuvent se produire en même temps, ce qui laisse croire que lorsqu'il y a une pénurie, elle implique souvent les deux éléments. La fraction de taille <3 μm est responsable d'une partie importante du déficit en P, alors que la fraction >3 μm l'est de la réaction facilitée par l'ammonium. Ainsi, la taille du plancton est un facteur important à considérer pour comprendre les carences nutritives des communautés planctoniques. Nos résultats mettent en évidence (*i*) l'importance de mesurer les carences proximales sur des échelles de temps plus longues, (*ii*) l'existence fréquente d'une carence conjointe de N et de P, (*iii*) la nécessité de définir les termes de restriction et de carence dans le contexte de la méthodologie utilisée et (*iv*) l'importance de faire plusieurs mesures concurrentes des carences afin d'évaluer le statut nutritif des communautés planctoniques.

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Introduction

A central objective of limnological research has been to understand and predict the abundance and composition of phytoplankton. Studies examining phytoplankton–nutrient interactions have dominated this research because nutrients play a fundamental role in the limitation of algal production and biomass. The role of P is central to our current understanding of phytoplankton abundance and distribution in lakes (Schindler 1978; Hecky and Kilham 1988). Phosphorus limitation in lakes is supported by many studies and is important with respect to both community biomass (Dillon and Rigler 1974) and community composition (Watson et al. 1997). However, N is also important and may have a secondary role in limiting community abundance and affecting species distribution (Smith 1982; Hecky and Kilham 1988; Elser et al. 1990).

Studies assessing limitation have generally compared phytoplankton biomass and species composition in lakes across nutrient gradients or have conducted nutrient addition

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experiments. Other studies have sought to demonstrate nutrient deficiency in unmanipulated lakes (Healey and Hendzel 1980). There is a fundamental distinction between knowing how lakes respond to a perturbation (e.g., nutrient addition) and knowing how lakes function without manipulation. The concept of ultimate versus proximate nutrient limitation highlights this difference. Ultimate nutrient limitation of lakes must be considered over longer time scales (months to decades) and is paramount to understanding biomass and production at the temporal scale. Proximate nutrient limitation, on the other hand, concerns the growth or physiological status of algal species (Healey 1979) at a specific time and place within a lake.

During summer stratification in many temperate lakes, biological uptake often drives inorganic nutrient concentrations to near or below detection limits. Under these circumstances, availability of dissolved inorganic nutrients should be an important variable controlling phytoplankton species composition and productivity. On the other hand, the total amount of a nutrient present (especially total P (TP) and total N (TN)) plays a key role in determining the carrying capacity or potential attainable biomass. This relationship is exemplified by the abundance of published TP versus chlorophyll *a* (Chl *a*) relationships (e.g., Dillon and Rigler 1974; Organisation for Economic Co-operation and Development 1982; McCauley et al. 1989). Thus, ultimate limitation is best viewed as the total concentration of a limiting nutrient with respect to biomass (i.e., yield sensu Liebig, Odum 1997), whereas nutrient deficiency is best viewed in the proximate sense of limiting instantaneous growth rates (Beardall et al. 2001). The distinction between limitation and deficiency is critical because limiting nutrients do not necessarily equate to deficient nutrients for all phytoplankton at all times and places (De Baar 1994; Beardall et al. 2001). A deficient nutrient, while available, may be energetically costly to obtain (e.g., N_2 for N-fixing cyanobacteria).

Nutrient ratios have been used as a basis for evaluating nutrient limitation for several decades. Plankton nutrient ratios originally were found to be similar across much of the world's oceans (Redfield 1958). The consistency of nutrient ratios in the ocean was postulated to result from the interaction between elemental requirements of plankton and available nutrient pools resulting from biogeochemical nutrient cycling (Redfield 1958). Studies have since shown that these ratios often deviate across the oceans (Hecky et al. 1993; Falkowski 2000), but the original ratio postulated by Redfield is still used as a benchmark for comparison. Since inorganic C is available in excess, deviations from Redfield's ratio of 106:16:1 (C:N:P molar ratio) result from limitation in either N or P, intracellular nutrient storage, or detritus. Particulate nutrient ratios, especially N:P and C:N, are thought to be one of the simplest measures of phytoplankton nutrient status, although deviations from the Redfield ratio are common in lakes (Hecky et al. 1993).

One distinction between bioassay experiments and total nutrient ratios is that total nutrient ratios represent an integrated measure of nutrient availability over longer time scales (Redfield 1934; Kilham 1990; Falkowski 2000), whereas bioassays, such as N and P debt, alkaline phosphatase activity, and PO_4^{3-} turnover time measure deficiency at shorter time scales (Healey 1975, 1979). Total nutrient ratios, therefore, should provide better indices of nutrient limitation, whereas physiological assessments should be more reflective of nutrient deficiencies. Particulate nutrient ratios often reflect total nutrient ratios (Hecky et al. 1993), but since they are a measure of organism stoichiometry, they may also reflect nutrient deficiencies. It is important to note that limitation and deficiency are not mutually exclusive with respect to any one nutrient and it is not uncommon for a limiting nutrient to also be deficient (Hecky et al. 1993). Therefore, within both a community and a species, more than one nutrient can be deficient at the same time.

Morphological and physiological differences between plankton result in different nutrient competitive abilities (Tilman 1982). Other attributes aside, small plankton and those with large surface area to volume ratios have an advantage in nutrient uptake. Bacteria have been shown to be especially proficient at taking up PO_4^{3-}, and bacteria-sized particles (<3 µm) account for most of phosphate uptake in the epilimnion of P-limited lakes (Currie and Kalff 1984; Mazumder et al. 1988; Taylor and Lean 1991). Studies also suggest that in many instances, bacteria may be limited by P and not organic C (Toolan et al. 1991; Coveney and Wetzel 1992). The proportion of P and N deficiency accounted for by bacteria-sized particles is, therefore, important for understanding the dynamics of both the plankton community as a whole and larger phytoplankton.

The purposes of the study presented are to (*i*) better understand the role of nutrients (N and P) in plankton communities of British Columbia lakes and reservoirs, (*ii*) examine the role and magnitude of both nutrient limitation and seasonal nutrient deficiency, (*iii*) assess the relative importance of bacteria/picoplankton and >3 µm size fractions in nutrient deficiency bioassays, and (*iv*) examine the correspondence of different methods of assessing nutrient limitation and deficiency. Nitrogen and P were considered because of their general importance in nutrient studies and specific studies suggesting both N and P limitation in coastal lakes (e.g., Suttle and Harrison 1988).

We examined the above questions in lakes and reservoirs located on Vancouver Island and in the East Kootenay region of British Columbia. Phosphorus and N deficiency were examined in two plankton size classes (<3 and >3 µm) at least monthly during the stratified summer season and at least once during winter. Three measures of P limitation (TN:TP, particulate C (PC) : particulate P (PP), and particulate nitrogen (PN) : PP), one measure of P deficiency (P debt), one measure of N limitation (PC:PN), and two measures of N deficiency (N debt and ammonium-enhanced ^{14}C uptake response (AER)) were used. Phosphorus and N debt bioassays were developed using chemostat and batch culture experiments of Healey and Hendzel (1979, 1980). They measure dark uptake at saturating concentrations of PO_4^{3-} and NH_4^+ standardized to Chl *a*. The principle is that nutrient deficiency results in high capacity for uptake in the dark. AER is based on the enhanced dark fixation of C in the presence of NH_4^+ and indicates N deficiency (Yentsch et al. 1977; Mitchell 1989). The principle behind AER is that C skeletons are required for the incorporation of N into amino acids, so N-deficient cells in-

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crease their dark C fixation rates compared with N-replete cells (Elrifi and Turpin 1987).

Methods

Study sites, sampling, and chemical analysis

Six lakes and reservoirs near Victoria, British Columbia (coastal), and four lakes and reservoirs near Cranbrook, British Columbia (interior), were sampled and tested for plankton nutrient deficiency (Table 1). The coastal lakes are best classified as temperate warm monomictic and the interior lakes are temperate dimictic lakes. During winter, the coastal lakes reach a minimum water temperature of approximately 4 °C and, if it occurs, ice cover is typically transitory. Summer temperatures reach a maximum of 20–25 °C in both the coastal and interior lakes. We provide a summary of the lakes, their locations, and basic morphological and limnological parameters (Table 1).

Each lake was sampled at its point of maximum depth; Shawnigan Lake and Sooke Lake reservoir were sampled at the point of maximum depth in two different basins because they each have morphometrically and hydrodynamically distinct basins. Coastal lakes were sampled monthly from May to September in 2000 and from May to November in 2001 and during the winter (January–February) of 2001 and 2002. Shawnigan Lake and Sooke Lake reservoir were sampled every 2 weeks during the summer of 2001. Interior lakes were sampled three times during 2000 (May, July, and September). Temperature profiles (YSI model 58) were used to define epilimnetic and metalimnetic layers. An integrated epilimnetic sample was taken using a 5 cm diameter, 6-m length of Tygon tubing with a weight attached at one end. Epilimnetic samples were taken over the whole epilimnion if it was <5.5 m deep or otherwise the top 5.5 m. Metalimnetic samples were taken near the centre of the metalimnion using a Niskin bottle. Triplicate water samples were taken from both the epilimnion and metalimnion. Secchi depth measurements were taken with a 20-cm black and white Secchi disk (Table 1).

Light extinction coefficients for photosynthetically available radiation (PAR) were determined using a 2π quantum sensor (LI-COR LI-192SA). PAR measurements were made at least every metre through the mixed layer. Measurements of PAR in air were made prior to and after underwater measurements to ensure that the incident light remained similar. Extinction coefficients (k) were calculated from the slope of the linear regression of the logarithm of light versus depth. Mean mixing layer irradiance ($\bar{I}$) was calculated using the same formula as Guildford et al. (2000):

$$\bar{I} = I_s((1 - e^{-kZ_m})(kZ_m)^{-1})$$

where I_s is the sum of daily incident solar PAR. The I_s was measured only on Vancouver Island. The sensor (LI-COR LI-90SZ) was at the top of the drinking water intake tower on Sooke Lake reservoir. To integrate variation due to cloud cover, I_s was averaged 1 week before and 1 week after k was measured and adjusted for 6% surface reflectance (Wetzel and Likens 2000). During winter, the coastal lakes do not freeze, so mixing depth (Z_m) for determining mean epilimnetic PAR was defined as the shallower of the surface to (but not including) the depth where the temperature changed by 0.5 °C over 0.5 m or the mean depth of the lake. An average daily (24 h) limitation threshold for $\bar{I}$ of 58.3 µmol quanta·m^{-2}·s^{-1} was used; below this value, algae in the mixed layer were considered to be light-limited (Hecky and Guildford 1984).

Chl *a* was analyzed by filtering samples through GF/F filters (Whatman) and then extracting the filters with 95% ethanol at 4 °C overnight and analyzing the extracts on a spectrophotometer (Ultrospec® 2000, Amersham) using a 10-cm quartz cell. Chl *a* was calculated according to Wintermans and De Mots (1965). A VWR pH probe (model 2000) was used to determine pH. TP, total dissolved P (TDP), TN, and NO_3^-/NO_2^- were analyzed on a Lachat automated ion analyzer (Zellweger Analytics, QuickChem® 8000). NH_4^+/NH_3 was analyzed manually on a spectrophotometer (Stainton et al. 1977). TP was measured by digesting unfiltered samples in an autoclave with potassium persulfate. The digested phosphate was analyzed using the ascorbic acid method (American Public Health Association 1998). TDP was determined by filtration through 0.45-µm membrane filters and analysis of the filtrate as for TP. TN was measured by autoclaving unfiltered samples with an alkaline potassium persulfate solution. After digestion, samples were measured as nitrite using the cadmium column reduction method (American Public Health Association 1998). NO_3^-/NO_2^- was analyzed using water filtered through 0.45-µm membrane filters and measured using the cadmium reduction method. Particulate nutrients were measured only from the epilimnion. PC and PN were collected on precombusted GF/Fs and analyzed on a CHN analyzer (Costech) with a Delta^{plus} Advantage mass spectrometer as the detector. Standard curves using acetanilide were generated for each run. PP was collected on acid-rinsed membrane filters (0.2 µm pore size) and analyzed in a similar manner to TP. Average dissolved and total nutrients, Chl *a*, and pH were determined from triplicate water samples, while particulate analysis was estimated from one sample. The test of discordancy (Barnett and Lewis 1984) was used to identify and remove outliers from samples conducted in triplicate.

Nutrient deficiency bioassays

Nutrient status of plankton was evaluated using six different methods (Table 2). PC:PN was used as a measure of N limitation, and PC:PP and N:P (TN:TP and PN:PP) were used as measures of P limitation. Phosphorus and N debt assays were used as indicators of nutrient deficiency of P and N, respectively (Healey 1975), and AER was used as a measure of N deficiency (Yentsch et al. 1977; Mitchell 1989).

Phosphorus and N debt bioassays were conducted according to Healey (1975) and Healey and Hendzel (1979, 1980). Glassware for all nutrient bioassays was acid-washed in 10% HCl, rinsed with deionized water six times, and placed in a drying oven. Phosphorus and N debt were conducted on all samples collected in 2000 until the winter of 2002. Water was pooled from the triplicate water samples and bioassays were conducted on this combined sample. Bioassays were conducted on both unfiltered water and water filtered gently through 3-µm polycarbonate filters (AMD Manufacturing Inc.). Filtered water was divided into separate flasks for P and N debt. Na_2HPO_4 and NH_4Cl were added to the samples to a final concentration of approximately 5 µmol·L^{-1}. Nutrient analyses for P and N debt were conducted manually with

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Table 1. Morphological and limnological characteristics of lakes and reservoirs in this study.

Lake	Location	Surface area (ha)	Max. depth (m)	Mean depth (m)	Secchi (m)	pH	DOC ($mg \cdot L^{-1}$)	Chl *a* ($\mu g \cdot L^{-1}$)	TP ($\mu g \cdot L^{-1}$)	TN ($\mu g \cdot L^{-1}$)	PC:PN (molar ratio)	PC:PP (molar ratio)	PN:PP (molar ratio)
Council Lake	48°31′N, 123°40′W	16	17.0	5.2	8.3	7.5	2.1	0.9	3.6	96.0	12.4	312	26.0
Cusheon Lake	48°48′N, 123°28′W	31	9.5	4.4	3.8	7.6	5.2	5.9	16.1	417.6	8.8	202	24.2
Elk Lake	48°31′N, 123°23′W	246	20	7.7	5.0	8.2	5.4	2.9	17.6	401.5	9.0	200	21.8
Jimsmith Lake	49°28′N, 115°50′W	21	7.5	4.9	6.0	8.4	7.7	1.4	8.9	368.2	15.7	489	28.9
Mark Creek reservoir[a]	49°41′N, 116°01′W	5	17.5	5.8	7.2	7.4	2.2	0.8	4.6	59.8	17.7	457	26.9
Maxwell Lake[a]	48°49′N, 123°31′W	27	17.0	6.5	4.6	7.2	4.6	2.4	9.6	257.9	9.8	244	24.5
New Lake	49°30′N, 115°50′W	27	10.5	3.0	5.2	8.4	18.0	2.3	10.3	1077.7	17.5	484	27.3
Phillips Lake reservoir[a]	49°27′N, 115°42′W	30	17.5	7.7	6.2	8.5	2.0	0.8	7.2	112.9	16.6	354	21.6
Shawnigan Lake	48°37′N, 123°38′W	552	53.0	13.0									
Shawnigan Lake north basin		359	53.0	14.2	5.9	7.5	3.1	1.7	4.9	152.4	11.7	357	30.2
Shawnigan Lake south basin		57	27.0	11.9	5.9	7.5	3.1	1.6	4.4	153.4	11.7	406	35.4
Sooke Lake reservoir[a,b]	48°33′N, 123°41′W	605	70.0	19.5									
Sooke Lake north basin[a,b]		434	70	23.2	8.5	7.5	2.1	0.7	3.1	80.9	12.2	274	23.7
Sooke Lake south basin[a,b]		45	22	8.6	7.4	7.4	2.0	0.9	3.3	85.6	12.2	319	27.0

Note: Area, maximum depth, and mean depth are for full stage conditions. Secchi, pH, DOC (dissolved organic C), Chl *a*, TP, TN, PC:PN, PC:PP, and PN:PP are summer epilimnetic averages (May–September). For comparison, Redfield ratios are 6.6:1 for PC:PN, 106:1 for PC:PP, and 16:1 for PN:PP. Shawnigan Lake and Sooke Lake reservoir each have three major basins; the two sampling stations were in the north and south basins. Morphometric data are from Spafard et al. (2002).

[a]Reservoirs and lakes that may experience seasonal drawdown.

[b]Sooke Lake reservoir physical parameters are valid from 1989 when the dam was last raised until winter 2003 when the dam was again raised.

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Table 2. Values for phytoplankton nutrient limitation and deficiency thresholds.

Indicator	Nutrient	Deficiency threshold
C:N[a,b]	N	>14.6 (molar ratio)
C:P[a,b]	P	>258 (molar ratio)
N:P[a,b]	P	>22 (molar ratio)
P debt[c]	P	>0.075 μmol P μg Chl a^{-1}·day^{-1}
N debt[c]	N	>0.15 μmol N μg Chl a^{-1}·day^{-1}
Dark NH_4^+-enhanced ^{14}C uptake[c]	N	>0.02 μg C μg Chl a^{-1}·h^{-1}, >2 ($+NH_4^+$/$-NH_4^+$)

Note: Adapted from Guildford and Hecky (2000).
[a]Healey (1975) and Healey and Hendzel (1980).
[b]Particulate ratios.
[c]Mitchell (1989) and Yentsch et al. (1977).

a spectrophotometer using the ascorbic acid and Berthelot reaction methods, respectively (Stainton et al. 1977). Triplicate (P debt) and quadruplicate (N debt) measurements were taken immediately after spiking the samples and again after incubating samples in the dark at room temperature for 24 h. Deficiency values used for nutrient debt assays are from Healey (1975) and Healey and Hendzel (1980).

AER bioassays were conducted on epilimnetic samples from coastal lakes and reservoirs from July 2001 to the winter of 2002. Dark inorganic ^{14}C incubations were conducted in a manner similar to that outlined by Shearer et al. (1985). The water source used for these bioassays was the same as that used in nutrient debt bioassays. Incubations were conducted in 65-mL glass bottles without headspace. Four hundred millilitres of water were spiked with 0.8 mL of $NaH^{14}CO_3^-$ to a final activity of 590 kBq. Samples were gently mixed using a magnetic stirrer and three subsamples were removed and incubated. Immediately after these samples were removed, 1 mL of 1 mmol $NH_4Cl{\cdot}L^{-1}$ was added to the remaining lake sample (final concentration of NH_4^+ was approximately 5 μmol·L^{-1}) and this was stirred before being transferred to three separate incubation bottles. Incubations were conducted for 4.5–5 h (Elser et al. 1988) at approximately in situ lake temperatures. Immediately following incubation, 3 mL was transferred from incubation bottles to scintillation vials containing a CO_2 trapping agent (3-methoxypropylamine, Fluka). The 3-mL sample was used to determine the total available ^{14}C in each sample. The remaining water in the incubation bottles was filtered through 0.45-μm Gelman membrane filters. Filters were fumed in a desiccator with concentrated HCl before being transferred to scintillation vials and counted (Beckman LS6000IC).

Alkalinity of each sample was determined using Gran titration, and dissolved inorganic C was calculated from pH and alkalinity (Park 1969). Carbon uptake rates were determined by solving the following equation (Wetzel and Likens 2000):

$$\text{C fixation} = \frac{^{14}\text{C assimilated} \times {}^{12}\text{C available}}{^{14}\text{C available}} \times 1.06$$

where ^{14}C assimilated is the disintegrations per minute of the particulates per millilitre, ^{14}C available is the total disintegrations per minute per millilitre, ^{12}C available is dissolved inorganic C per litre, and 1.06 is an isotope correction factor. AER ratios (Yentsch et al. 1977) were calculated by dividing the average rate of C fixation (micrograms of C per microgram of Chl *a* per hour) of samples incubated with added NH_4^+ ($+NH_4^+$) by the average of those incubated without NH_4^+ ($-NH_4^+$).

The threshold ratio of 2, defining N limitation using AER, was somewhat arbitrarily assigned by Yentsch et al. (1977). Mitchell and Malthus (1984) found that ratios <1.5 were significantly different and may represent N deficiency. Mitchell (1989) suggested that C fixation rate measurements represent a more robust means of evaluating N limitation and proposed the threshold enhancement rate of 0.02 μg C μg Chl a^{-1}·h^{-1}.

Whole water and <3 μm size fractions were incubated for all of the physiological nutrient assays. The <3 μm size fraction was subtracted from the whole-water lake samples to calculate the nutrient status of the >3 μm size fraction. On occasion, the <3 μm size fraction had a slightly greater response than the whole water. When this occurred, the >3 μm fraction was assumed to have zero deficiency. Chlorophyll was not fractionated during the study, so only the relative proportion that these two size fractions contributed to the total deficiency of each bioassay could be assessed because the fractionated Chl *a* biomass corrected rates were unavailable for comparison with the nutrient thresholds (Table 2). Pearson's correlation was used to describe the relationship between AER ratios and AER rate measurements.

Results

AER measurements are usually analyzed as either an enhancement ratio or an enhancement rate. Comparison of whole-water AER, as expected, showed that these two analyses were well correlated ($r^2 = 0.84$) (Fig. 1*a*). An enhancement ratio of 2 (Yentsch et al. 1977) corresponded to an enhanced fixation rate of 0.05 μg C μg Chl a^{-1}·h^{-1}, while an enhanced fixation rate of 0.02 μg C μg Chl a^{-1}·h^{-1} (Mitchell 1989) corresponded to an enhancement ratio of 1.42. The <3 μm size fraction was enhanced by a ratio of more than 1.42 on only two dates (2.16 on 16 July 2001 and 1.42 on 16 October 2001, both in Shawnigan North). However, the <3 μm size fraction did account for a large proportion (mean = 62%, range from 28% to 90%) of the total dark C fixation (Table D1[1]). Thus, enhancement ratios for the >3 μm size

[1] Supplementary data for this article are available on the Web site or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Ottawa, ON K1A 0S2, Canada. DUD 3599. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml.

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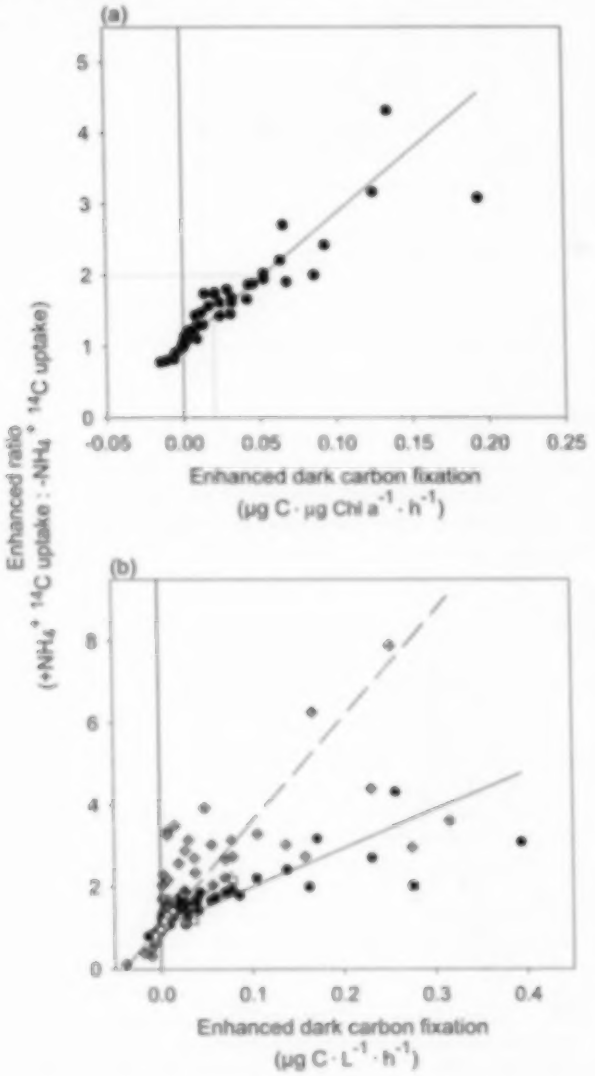
Fig. 1. (*a*) Chlorophyll-specific NH_4^+-enhanced ^{14}C uptake response (AER) enhancement rates versus AER ratios for whole water (ratio = rate × 18.13 + 1.05, $r^2 = 0.84$). The horizontal broken line represents an uptake deficiency threshold ratio of 2 (Yentsch et al. 1977) and the vertical broken line represents an enhancement deficiency threshold rate of 0.02 μg C μg Chl $a^{-1} \cdot h^{-1}$ (Mitchell 1989). (*b*) Comparison of absolute enhancement rates for different size fractions. Squares, <3 μm; diamonds, >3 μm; circles, whole water. Lines of best fit were determined using bivariate principle axes analysis.


(a)
Enhanced ratio
(+NH4+ 14C uptake : -NH4+ 14C uptake)
Enhanced dark carbon fixation
(μg C · μg Chl a-1 · h-1)
(b)
Enhanced dark carbon fixation
(μg C · L-1 · h-1)

fraction are higher because the <3 μm size fraction component was subtracted from whole water (Fig. 1*b*).

A comparison of AER and N debt in the >3 μm size fraction showed a weak correlation ($r^2 = 0.35$, $p < 0.01$). This comparison was conducted using volumetric rates (Fig. 2) because we do not have measurements of the >3 μm chlorophyll fraction. Nitrogen-deficient samples are marked with either "+" (AER) or "∝" (N debt). Overall, AER appeared to be a more sensitive measure. Of the 54 samples with results from both nutrient assays, 38 had zero net N debt uptake in the >3 μm size fraction, while only seven had no >3 μm size fraction AER.

Seasonal water column mean irradiances for Council Lake, Shawnigan Lake, and Sooke Lake reservoir suggest that light was not limiting photosynthesis in the mixed layer from May to October (Fig. 3). The same trend was found for the other coastal lakes (data not shown).

TN:TP of the epilimnion and metalimnion suggest that if or when our study lakes were nutrient-limited, P was most likely limiting (Fig. 4). Average particulate ratios are greater than Redfield ratios (Table 1) and PC:PN was high in interior lakes (Jimsmith, Mark Creek, New, and Phillips). Other ratios fall within the typical range of north-temperate lakes (Hecky et al. 1993; Guildford and Hecky 2000). Jimsmith Lake and New Lake (interior lakes) had the greatest average TN:TP and high PC:PP. Both Jimsmith Lake and New Lake have extensive macrophyte communities, which may partly explain the relatively high particulate C concentrations. Overall, PN:PP ratios were lower than TN:TP, with a few points falling below the Redfield ratio (Fig. 4*a*). Data for PC:PP fell on both sides of the threshold line (Fig. 4*c*). PC:PN, a measure of N limitation, suggested that the plankton communities were also N-limited on some dates, although most points fall below the threshold line (Fig. 4*d*). Measures of N and P debt and AER corroborate that plankton communities were both P- and N-deficient (Fig. 5). Phosphorus debt was associated with limiting TN:TP ratios, which was not surprising because on most dates, TN:TP was considered to be P limiting (Fig. 5*a*). Many samples that showed N deficiency (N debt and AER) were also P-limited according to TN:TP (Figs. 5*a* and 5*b*). There was not a clear trend observed between increasing deficiency as indicated by the bioassays and the particulate ratio limiting thresholds (Figs. 5*d*–5*f*). However, severe deficiency determined using bioassays was observed to occur at elemental ratios nearer to Redfield (Fig. 5*d*–5*f*) than is commonly assumed (Table 2).

As expected, nutrient debt was greater when dissolved nutrients were low (Fig. 6). Note that TDP was used in this comparison because dissolved inorganic P measurements were routinely near zero (below our analytical detection limit). When dissolved inorganic P is low, the ascorbic acid method is known to give overestimates (Hudson et al. 2000). Deficiency, especially of P, was more pronounced in the epilimnion (Fig. 6*a* versus Fig. 6*b*). The concentrations of dissolved inorganic N and TDP above which nutrient deficiency was not observed are similar to the limiting resource thresholds of growth for NO_3^- (approximately 7.1 μmol·L^{-1}) and PO_4^{3-} (approximately 0.27 μmol·L^{-1}) reported by Interlandi and Kilham (2001). On average, most of our N bioassays were deficient at lower values of dissolved inorganic N than the threshold reported by Interlandi and Kilham (2001), but our P debt assay is in close agreement.

Both size fractions usually contributed to the total deficiency for N and P debt of those epilimnetic samples that were considered to be nutrient-deficient (i.e., greater than deficiency threshold). The <3 μm size fraction most frequently contributed more than half of the total P debt (Fig. 7). On the other hand, AER was principally a result of the >3 μm size fraction. When AER occurred in the <3 μm size fraction, it was usually small and was not considered

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Fig. 2. Nitrogen debt versus NH_4^+-enhanced ^{14}C uptake response (AER) for all dates when both N debt and AER assay were conducted. All points are represented by a circle. When either whole-water N debt or AER was considered to be deficient, the contribution of the >3 μm size fraction is noted with either "+" (AER) or "×" (N debt). If both the AER and N debt indicated deficiency, then the circle is solid. $r^2 = 0.35$, $p < 0.01$.

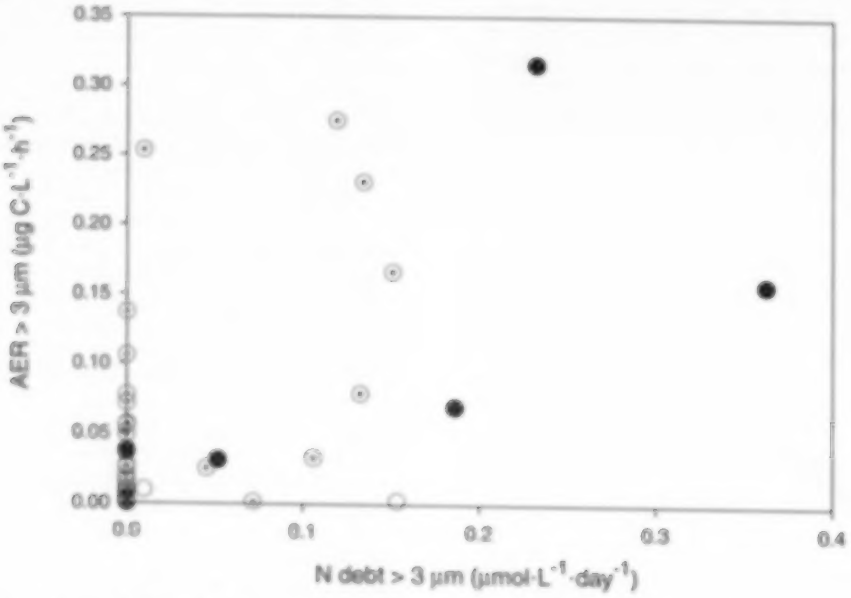
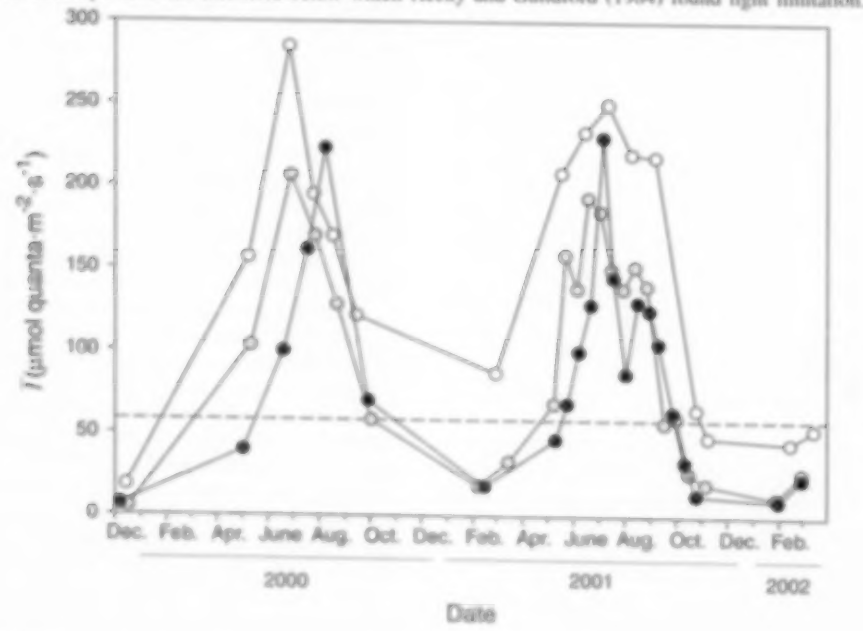


Fig. 3. Daily mean water column photosynthetically available radiation (PAR) of the mixed layer, $\bar{I}$, in Council (open circles), Shawnigan (shaded circles), and Sooke (solid circles) lakes. Solar incident PAR was measured and corrected for 6% surface reflectance. The broken line represents the threshold below which Hecky and Guildford (1984) found light limitation.



deficient. Over a third of samples had <25% of N debt accounted for by the <3 μm size fraction, while the <3 μm size fraction accounted for more than 75% of the total N debt in 41% of the samples. Like AER, these latter deficiencies were usually close to threshold values.

Seasonal patterns in nutrient deficiency were examined in North Shawnigan Lake and Sooke Lake reservoir (deepest stations) because these sites were sampled every 2 weeks during the summer (2001). These lakes are in close proximity (within 4 km) and have many similar limnological pa-

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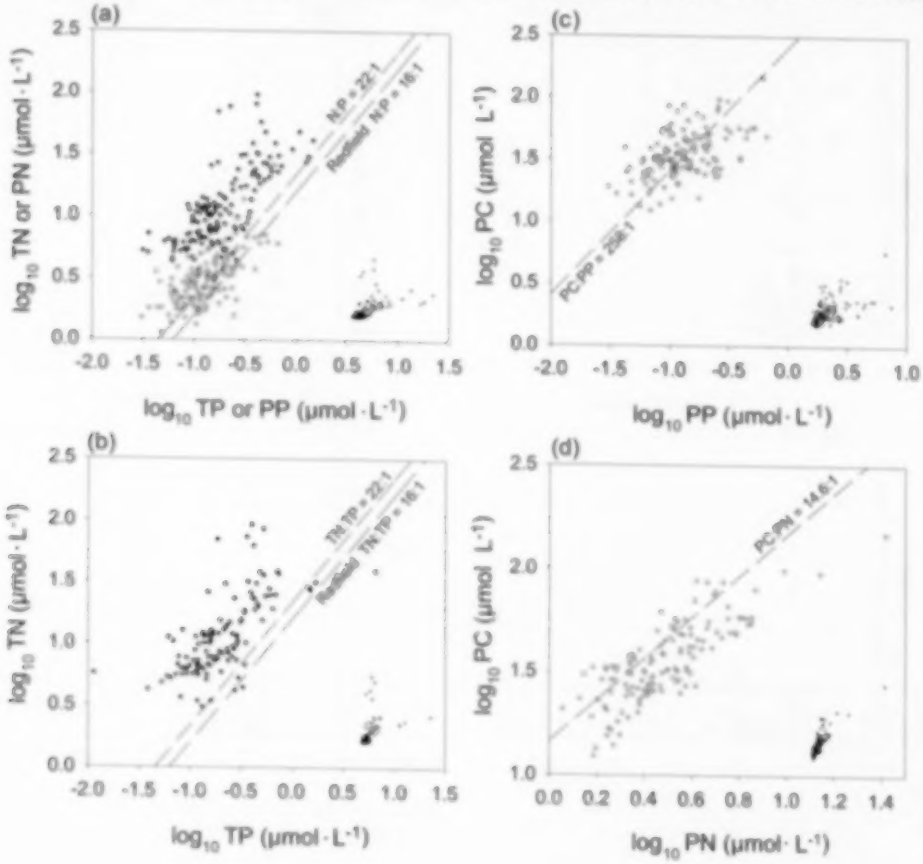
Fig. 4. Total N versus total P for (*a*) the epilimnion and (*b*) metalimnion of all study lakes during stratified periods. Particulate comparison of (*c*) particulate C (PC) versus particulate P (PP) and (*d*) particulate N (PN) versus PP are given for epilimnetic samples. Inset figures show the non-log-transformed data. Inset figure in Figure 4*a* is for total nutrients only. Broken lines are the 22:1 and 16:1 N:P ratios (molar) for N versus P (Figs. 4*a* and 4*b*), 258:1 for the PC:PP ratio (Fig. 4*c*), and 14.6:1 for PC versus PN (Fig. 4*d*).



rameters (Table 1). Despite this, there were noticeable differences in nutrient deficiency measures. Both showed P debt during the summer months, but in Shawnigan, the >3 µm size fraction was consistently deficient from early July until late September, while the <3 µm size fraction constituted a consistent proportion of the total debt (Fig. 8*a*). Sooke Lake reservoir was extremely P-deficient from late May until mid-July (Fig. 8*b*). However, unlike Shawnigan, the <3 µm size fraction accounted for most of the P debt during this time.

One of the lakes that showed a consistent annual pattern of N debt over the 2 years of our study was Council Lake. Council Lake has high TN:TP for most of the year (mean = 64.3 ± 5.8 SE) but was strongly N-deficient (N debt assay) during the spring, with the deficiency decreasing over the course of the summer (Fig. 9). Despite relatively high TN:TP, dissolved inorganic N was <1 µmol·L^{-1} for all dates except February 2000. TDP concentrations were also low, <0.1 µmol·L^{-1}, for all dates except May 2001. Phosphorus debt indicated that Council Lake plankton were frequently P-deficient. Breaking the nutrient assays into >3 and <3 µm size fractions suggests that despite high TN:TP, the <3 µm size fraction often contributed a large proportion of the P debt (Fig. 9). Nitrogen deficiency for the >3 µm size fraction remained severe during the spring and early summer of both years. AER suggested strong N deficiency for the >3 µm size fraction in August and September 2001.

In general, plankton communities of the coastal lakes had higher nutrient debt during the summer and lower debt in the winter, although nutrient deficiency was noted to occur during the winter. None of the lakes exhibited enhanced AER during January and February. Three of our lakes did, however, have severe P debt during the winter (Council, Sooke North, and Shawnigan South). Apart from Council Lake in the winter of 2001, it was the >3 µm size fraction that contributed most of this P debt.

Discussion

TN:TP suggests that our lakes are P-limited, that is, the biomass of phytoplankton is ultimately controlled by P. Analysis of particulate ratios demonstrated that the plankton community was in actuality closer to threshold limits than the TN:TP suggested. Physiological indicators suggested

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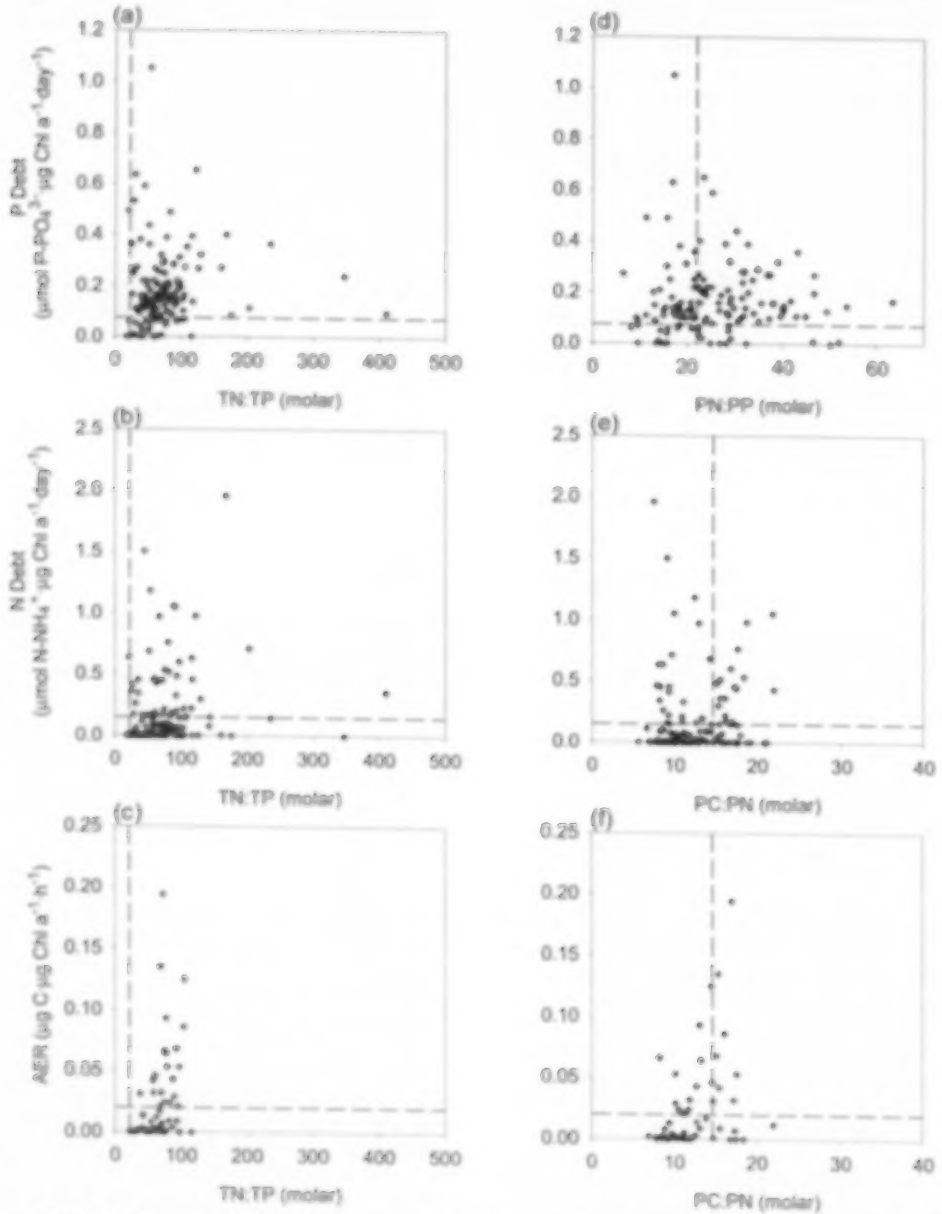
Fig. 5. Whole-water nutrient debt assays plotted against total N (TN) : total P (TP) molar ratios and particulate C (PC) : particulate P (PP) and PC : particulate N (PN) molar ratios. (*a*) P debt versus TN:TP; (*b*) N debt versus TN:TP; (*c*) NH_4^+-enhanced ^{14}C uptake response (AER) versus TN:TP; (*d*) P debt versus PN:PP; (*e*) N debt versus PC:PN; (*f*) AER versus PC:PN. Broken lines represent nutrient thresholds.



that both severe P deficiency and N deficiency occurred simultaneously. As such, TP may be ultimately limiting in our lakes, whereas particulate data may be more reflective of the plankton species composition that is most competitive under the particular resource supply ratios (Kilham 1990). Particulate ratios should more closely reflect deficiency bioassays; however, they do not necessarily reflect proximate nutrient deficiencies, since they are measures of biomass and not rate processes. Nutrient assays should reflect the proximate nutrient deficiencies of those plankton species and may in turn affect species competition. Hecky and Kilham (1988) suggested that the paradigm of N-limited oceans and P-limited lakes may be due in part to differences in technique. Because different techniques define limitation at different scales (*e.g.*, ultimate versus proximate), it is necessary that limitation studies consider the methods used and the implied time scales associated with the methods.

More than one nutrient seems to be deficient at a given time in a plankton community, which is illustrated temporally for three lakes. This suggests that in our coastal oligotrophic

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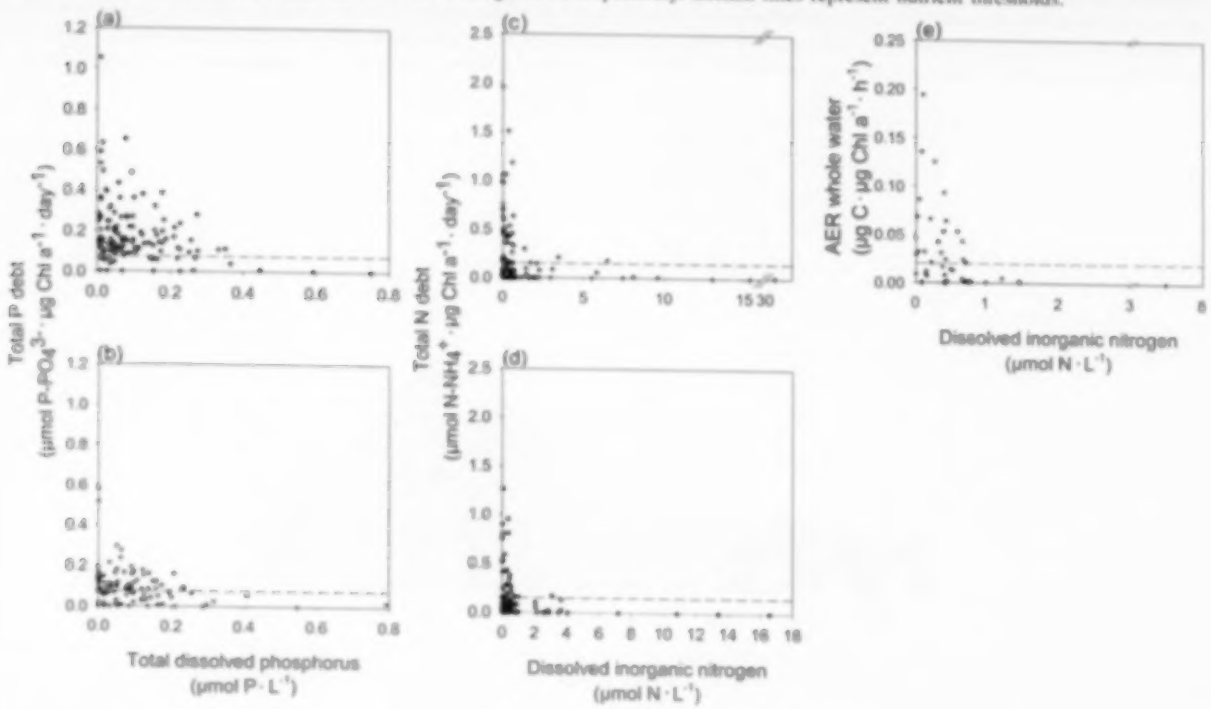
Fig. 6. Epilimnetic and metalimnetic (*a* and *b*) P debt and (*c* and *d*) N debt and (*e*) epilimnetic NH_4^+-enhanced ^{14}C uptake response (AER) versus total dissolved P and total dissolved inorganic N, respectively. Broken lines represent nutrient thresholds.



lakes during periods of nutrient stress, codeficiency may be a common occurrence rather than an exception. Phosphorus deficiency was more often dominated by the <3 µm size fraction, which corresponds to previous findings that bacteria have high P requirements. Nitrogen deficiency was not as clearly dominated by the <3 µm size fraction, and the AER assay suggests that, apart from a couple of days, the bacteria/picoplankton-sized fraction was not N-deficient.

Larger phytoplankton are at a disadvantage regarding dissolved nutrient uptake because they have greater volume to surface area ratios. Because dissolved nutrients (PO_4^{3-}, NH_4^+, and NO_3^-) were usually at low concentrations in the surface and metalimnetic waters of our study lakes, the larger phytoplankton must either grow more slowly, rely on luxury uptake and internal nutrient stores, or rely on phagotrophy. For example, many of the chrysophytes that are dominant in oligotrophic lakes are phagotrophic (Raven 1988; Jones 2000). Bacterial P has been found to serve as a substitute source of P for mixotrophic algae (Rothhaupt 1996). Jansson et al. (1996) suggested that N deficiency in larger plankton may be induced by mixotrophic consumption of P-rich bacteria. This offers one explanation for why phytoplankton show N deficiency despite high TN:TP. Phosphorus limitation itself may also offer an explanation for higher PC:PN, N debt, or AER in some of our samples, since extreme P limitation induces limiting PC:PN ratios in some phytoplankton species (Healey 1975).

While no two structural nutrients can limit (sensu stricto Liebig) the yield of a phytoplankton species at the same time (Odum 1997), more than one nonstructural nutrient can limit the growth rate (Tilman 1982; Odum 1997; Beardall et al. 2001). Deficiency of nonstructural nutrients (e.g., nutrients needed for enzymes and cofactors) will not directly affect the carrying capacity (i.e., potential yield) but will affect the rate at which phytoplankton will grow towards that yield. While we are not aware of clear empirical demonstration of colimitation by two nutrients for a single species, Healey (1985) demonstrated colimitation by nutrients and light, implying that energetic- or rate-limiting steps lower growth rate, regardless of the availability of structural nutrients. For example, iron deficiency in certain diatoms has been found

Fig. 7. Proportion of deficiency accounted for by the <3 µm size fraction for samples that were considered to be deficient. Solid bars, P debt; hatched bars, AER; open bars, N debt.

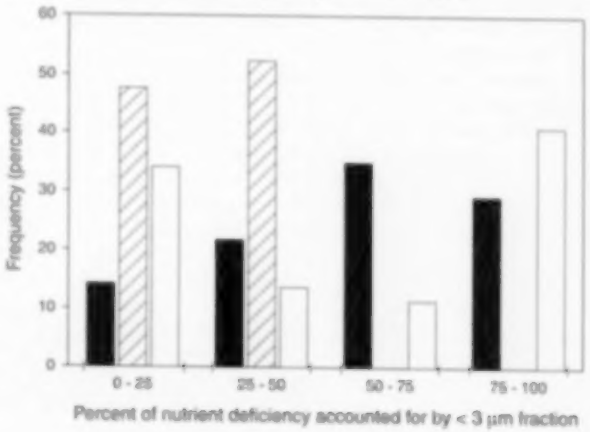


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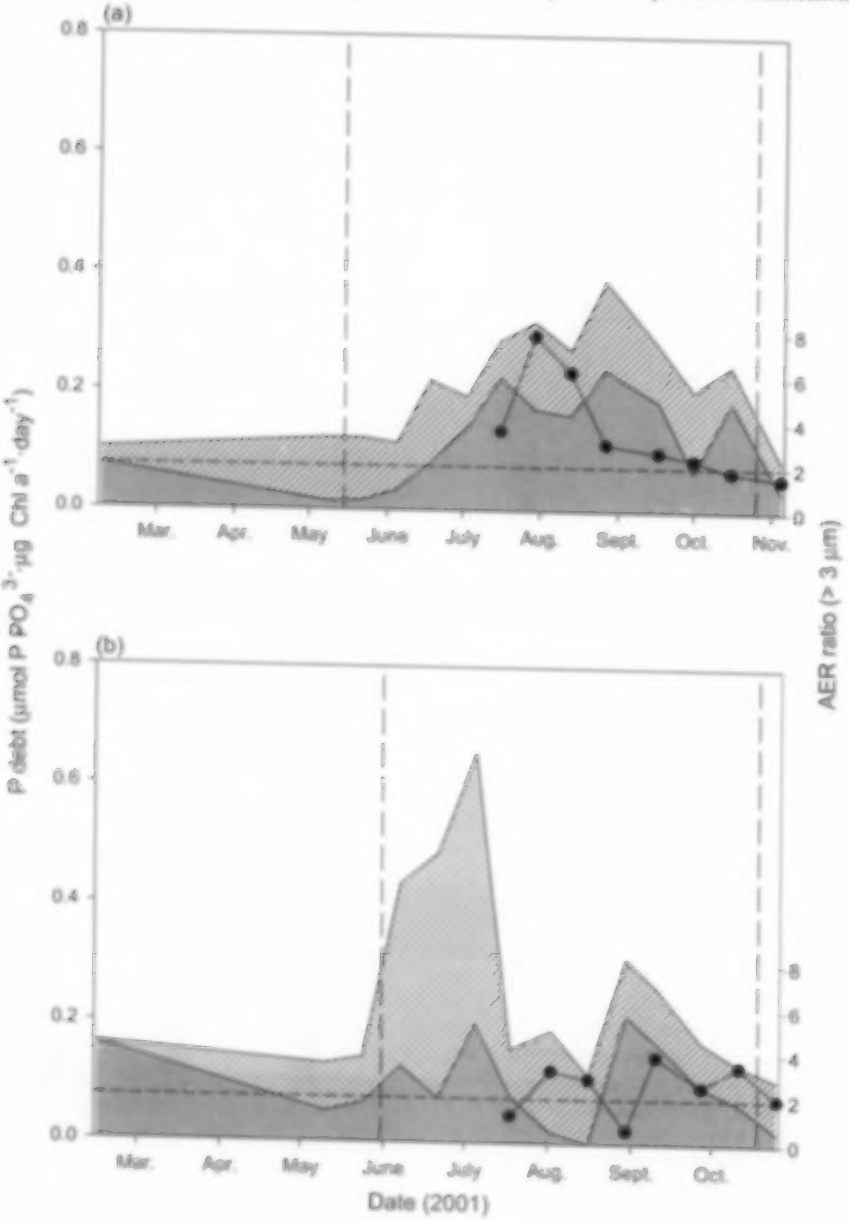
Fig. 8. Temporal size-fractionated epilimnetic P debt for (*a*) Shawnigan Lake north basin and (*b*) Sooke Lake north basin during 2001. Shaded, >3 μm size fraction; hatched, <3 μm size fraction. The sum of both is equal to the whole-water deficiency. The <3 μm size fraction was measured independently and is presented as a proportion of the whole-water deficiency with the >3 μm size fraction constituting the remaining amount. NH_4^+-enhanced ^{14}C uptake response (AER) for the >3 μm size fraction is represented by circles. The horizontal broken line represents the nutrient and the vertical broken lines represent the period of stratification.



to cause flavodoxin to be used in place of ferridoxin (La Roche et al. 1996). Thus, in theory, if iron is present in low concentrations, diatom growth rate would be reduced because of the lower energy efficiency of transfer of the photosystems while simultaneously being limited in yield by another nutrient. Lower growth rates resulting from iron deficiency may also affect the competitive ability of certain diatoms. While plankton diversity provides the most probable explanation for the codeficiency observed in this study, it is interesting to postulate about the idea of codeficiency within a single species, since nutrients required in the greatest amount usually have both structural and nonstructural roles. This study provides no direct evidence for this idea. However, it is interesting to note that severe P debt, N debt, and AER were

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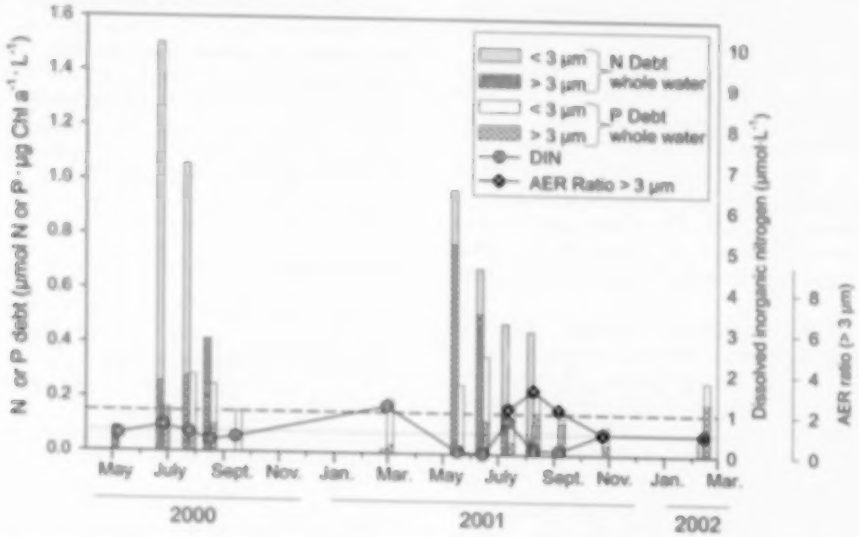
Fig. 9. Whole-water and size-fractionated seasonal trends in N debt, P debt, dissolved inorganic nitrogen (DIN), and NH_4^+-enhanced ^{14}C uptake response (AER) for Council Lake. The sum of both size fractions is equal to the whole-water deficiency. The <3 µm size fraction was measured independently and is presented as a proportion of the whole-water deficiency with the >3 µm size fraction constituting the remaining amount. The dashed horizontal line represents both the N debt and AER deficiency thresholds and the dotted line represents the P debt deficiency threshold.



observed to occur at particulate nutrient ratios closer to Redfield than the literature values used to define deficiency in this study.

An alternative explanation for N deficiency in lakes with high TN:TP is that dissolved organic N is less available than dissolved organic P. Allochthonous organic matter often has high N:P ratios (Wetzel 2001), so phytoplankton may still be N-deficient despite high TN:TP. Previous investigators (Healey and Hendzel 1980) found that nutrient ratios of plankton and detritus were not distinguishable, but there is a good possibility of interference in our lakes because TN:TP and PN:PP were poorly correlated ($r^2 = 0.001$). Both N and P turnover times remained rapid despite high N:P loading (50:1 molar ratio) in coastal British Columbia lakes (Suttle et al. 1991), corroborating our finding of N deficiency.

Bacteria are important with respect to nutrient uptake and affect bioassays both directly (e.g., representing a large percentage of P debt) and indirectly (e.g., masking enhancement effect in AER). Accounting for the bacterial component is critical if Chl *a* is used as the measure of biomass or when deficiency thresholds are derived from studies using axenic algal cultures. Correction for bacterial influence on larger plankton is most easily made by size fractionating chlorophyll and conducting bioassays on the bacteria-sized community in parallel with normal bioassays. Size fractionation of plankton has the unfortunate consequence of removing possible nutrient linkages, for example, micrograzer recycling of P that is utilized by bacteria. The magnitude of this effect was not measured in the current study; however, we believe that the contribution of bacterial P deficiency should be recognized when applying modelled nutrient thresholds and will allow for a more direct evaluation of deficiency severity in larger plankton. If a relatively large proportion of chlorophyll is in the <3 µm size fraction, but a larger proportion of nutrient deficiency is in the larger size fraction (>3 µm), then the larger size fraction will be more severely deficient than deficiency thresholds based on whole water would indicate.

Size fractionation is a convenient way of looking at different plankton functional groups (Sheldon et al. 1972). Although we looked at only two size fractions, the difference in P debt for Shawnigan Lake and Sooke Lake reservoir highlights the value of looking at these two sizes. During stratification, the >3 µm size fraction in Shawnigan Lake accounted for a large proportion of the P debt, whereas in Sooke Lake reservoir, the >3 µm size fraction accounted, on average, for much less of the total P debt. Overall, however, Sooke Lake reservoir showed greater P deficiency in June and July because of the large P uptake by the <3 µm size fraction. Since bacteria can dominate P uptake (Currie and Kalff 1984; Taylor and Lean 1991), it is important to clarify exactly what limitation bioassays represent.

The most striking differences in nutrient deficiency between the two size classes occurred in the AER assays. The threshold value for enhancement rates of 0.02 µg C·µg Chl $a^{-1}\cdot h^{-1}$ suggested by Mitchell (1989) corresponds to an enhancement ratio of 1.42 in this study, close to the significant ratio of 1.45 reported by Mitchell and Malthus (1984). AER deficiency threshold rates for just the >3 µm size fraction will typically be lower, whereas the threshold ratios will be higher than those obtained using whole water.

The most probable explanation for the lack of enhanced uptake by the AER <3 µm size fraction is that the size fraction was not N-deficient on most occasions. However, several potential explanations may account for these results. Dark inorganic C fixation results from anaplerotic carboxylation (Raven 1997). Under N limitation, these reactions provide C skeletons necessary for amino acids (Elrifi and Turpin 1987). Since the AER <3 µm size fraction was generally not enhanced, it suggests that (*i*) it was

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N-limited but used stored organic C as the C source, (*ii*) it had a means of storing N that does not require C uptake, (*iii*) it was N-limited but utilized a different N source (i.e., organic), or (*iv*) this size fraction was not N-limited. Since the <3 µm size fraction comprised a significant portion of the nonenhanced dark C fixation (mean = 62%, range from 28% to 90%), it is unlikely that cellular organic C would be exclusively used as the C skeleton source under NH_4^+-enhanced conditions. We are unaware of any studies demonstrating luxury dark N fixation that does not involve C. While this explanation cannot be ruled out, it is considered unlikely. However, N storage independent of C would offer an explanation for samples with high N debt and corresponding low AER. The <3 µm size fraction may have used organic N sources, but it is unlikely that it would not utilize NH_4^+ anaplerotically if it were deficient in N.

Every nutrient deficiency analysis is unique in how it measures and defines deficiency. This means that to better understand the nutrient status of a community, it is necessary to use several measures of deficiency and limitation. There was a weak relationship between severity of deficiency of the >3 µm size fraction for AER and N debt. The AER bioassay suggested greater N deficiency for most samples, either because the bioassay is more sensitive or because the thresholds for N debt and AER are not comparable. Guildford and Hecky (2000) found that N deficiency measures (N debt and C:N) did not follow a consistent pattern with either TN or TN:TP, whereas samples were consistently P-deficient when TN:TP was more than 50 (molar ratio). Nitrogen debt, therefore, may be less predictable with respect to TN:TP than P debt. This could be explained by the many different forms of N available and the demonstrated ability of plankton to store P.

The context of defining and measuring nutrient limitation is important for understanding plankton ecology. The lakes and reservoirs in our study are P-limited in an ultimate sense (as indicated by TN:TP ratios), although the actual plankton community itself reflected a lower ratio. Many of the study lakes and reservoirs demonstrated proximate deficiency of both N and P. When deficiency was exhibited, it was common for both N and P to be deficient at the same time. Suttle et al. (1991) found relative uptake rates in the <3 µm size fraction more P-limited, whereas the >3 µm size fraction was more N-limited. Using nutrient deficiencies, we found that the <3 µm size fraction constituted a large proportion of P debt, whereas the >3 µm size fraction constituted a large proportion of AER and N debt, which agrees with Suttle et al.'s (1991) results. These findings underscore the importance of both plankton size and time scales in defining the impact of nutrient deficiency and limitation in plankton communities. Previous studies have stressed the importance of N limitation under high TP (Smith 1982; McCauley et al. 1989); however, N deficiency may also be important for understanding phytoplankton distribution in lakes with low TP. The most fundamental observations from this study are the distinction between nutrient limitation and deficiency, that plankton communities can be codeficient in both N and P at a given time within a single lake, and that no single measure of deficiency reflects the complete nutrient status of the plankton community.

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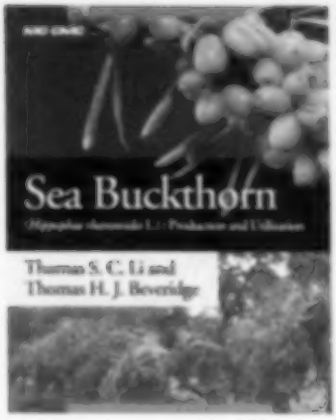

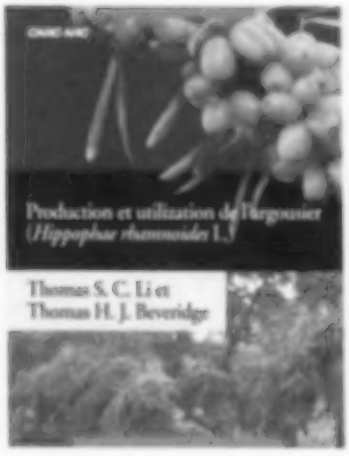

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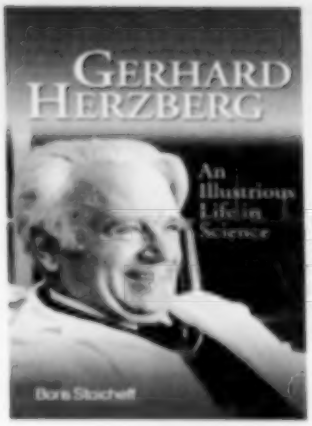

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